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Modern Systematic Studies in African Botany

Proceedings of the Eleventh Plenary Meeting of
the Association for the Taxonomic Study of
the Flora of Tropical Africa
Missouri Botanical Garden, St. Louis
June 10–14, 1985

Edited by Peter Goldblatt and Porter P. Lowry II

Association pour l'Etude Taxonomique
de la Flore d'Afrique Tropicale

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Missouri Botanical Garden

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Edited by
Peter Goldblatt, General Secretary, AETFAT
and
Porter P. Lowry II

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The AETFAT Secretariat was located at the Missouri Botanical Garden from 1982 to 1985, with Peter Goldblatt serving as the General Secretary. The Eleventh Plenary Meeting of the Association was held June 10–14, 1985 at the Missouri Botanical Garden and was attended by 125 visitors from Africa, Europe, and North America. The general theme of the Meeting was *Modern Systematic Studies in African Botany.*

The meeting and the publication of these proceedings was supported by grants from the United States National Science Foundation (BSR 84-18003), the Robert B. and Nancy M. Smith Fund for Tropical Botany, the Monsanto Fund, and by the Missouri Botanical Garden. Simultaneous English–French translation was made possible by a donation from Mrs. Raoul Pantaleoni. A grant from the US National Science Foundation International Programs Division, BSR 84-18203, supported the attendance of 12 participants from tropical African countries at the meetings and at a workshop in herbarium management, held at the Missouri Botanical Garden from 4–8 June.

The General Secretary thanks all those who assisted with the running of the Secretariat and the Plenary Meeting, particularly my assistant Debbie Wolfe, Pete Lowry, Hélène Le Dantec-Lowry, and Jeanne Zarucchi for help with social events and translation of abstracts and correspondence, and Janice Wilson for her work in editing the papers in this volume.

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STRUCTURES AND RELATIONSHIPS OF FAMILIES ENDEMIC TO OR CENTERED IN SOUTHERN AFRICA[1]

ROLF DAHLGREN[2] AND ABRAHAM E. VAN WYK[3]

ABSTRACT

Evidence (partly new) is summarized from various sources to evaluate critically the taxonomic status and relationships of some families mainly endemic to, or centered in, southern Africa, some also occurring widely outside this area. Androstachydaceae are not maintained as a distinct family; they have various features in support of inclusion in Euphorbiaceae. Achariaceae share features with both hypogynous (notably Flacourtiaceae and Passifloraceae) and with epigynous (notably Cucurbitaceae) families of Violales. Myrothamnaceae resemble Hamamelidaceae and Cercidiphyllaceae closely and are referable to Hamamelidales. The monotypic Geissolomataceae have many hamamelidalean features and should be placed in this order as well or in an adjacent unifamilial order. Bruniaceae and Grubbiaceae are anatomically similar to the two last-mentioned families, but both have unitegmic ovules and a few-celled nucellus, in which they resemble Ericales. It may be justified to treat them in a separate order, Bruniales. Greyiaceae are considered cunonialean-saxifragalean and are perhaps most closely related to the Francoaceae. Heteropyxidaceae are a distinct myrtalean family with similarities to Myrtaceae (secretory cavities, pollen) and Lythraceae (wood anatomy) but are embryologically distinct from both. Oliniaceae, Penaeaceae, and Rhynchocalycaceae are small closely related families, which, within the Myrtales, show the closest resemblance to Alzateaceae, Crypteroniaceae, and Memecylaceae, but to Lythraceae as well. Melianthaceae are sapindalean with similarities to both Sapindaceae and Anacardiaceae. Ptaeroxylaceae are rutalean in the strict sense and have affinities to Rutaceae and Cneoraceae, while the xerophytic Aitoniaceae, adapted to ornithophily and anemochory, should be included in Meliaceae. Roridulaceae and Stilbaceae are both regarded members of Scrophulariales (incl. Lamiales) and exhibit primitive features within that order. New embryological data settle the controversial question of the relationships of Retziaceae. It is placed among Stilbaceae, Scrophulariaceae, and Buddlejaceae in Scrophulariales. Lanariaceae are established as a new family to accommodate the morphologically isolated asparagalean genus *Lanaria*; whereas *Walleria*, with specialized seeds, is proposed to be treated in the asparagalean Tecophilaeaceae as a new subfamily Wallerioideae. Eriospermaceae, with a seed structure unique in monocotyledons, are considered to make up a distinct, isolated family in Asparagales, with their closest relationships uncertain.

RÉSUMÉ

Des données, en partie nouvelles, sont résumées à partir de sources diverses afin de permettre une évaluation critique de la position taxonomique et des relations de certaines familles pour la plupart endémiques à, ou centrées, dans le sud de l'afrique (certaines sont largement répendues en dehors de

[1] The authors wish to thank Dr. Peter Goldblatt for the invitation to work on this subject and for encouragement and help with the manuscript. R. Dahlgren acknowledges cooperation with J. Praglowski at the Natural History Museum, Stockholm, Sweden, in the pollen morphological studies of Geissolomataceae, Bruniaceae, Roridulaceae, Stilbaceae, Retziaceae, and *Walleria* (Tecophilaeaceae); the included photomicrographs of pollen grains of these families and *Bersama* (Melianthaceae) were prepared by him. Lu An-ming, Academia Sinica, China, working in cooperation with R. D. in Copenhagen, has contributed data on embryology in *Eriospermum* and prepared the pollen micrographs of this genus. Mrs. K. Engell, Institute of Plant Anatomy and Cytology, Copenhagen, has contributed the embryological information on *Retzia*, including the illustration material; T. Brogaard Nielsen, from the same department, has contributed further information on the embryology of *Grubbia* and *Brunia*. All the line drawings except for *Geissoloma* (made by R. D.) are originals made by B. Johnsen, Copenhagen. Mrs. A. Fox-Maule, Botanical Museum of the Copenhagen University, has checked the Latin diagnoses. Fixed material in FAA of Retziaceae, Bruniaceae, and Grubbiaceae has been supplied by Dr. I. Williams, Voëlklip, South Africa. P. Goldblatt, St. Louis, supplied material of *Roridula*. Cordial thanks are directed to all above-mentioned persons, as well as to S. Carlquist and R. F. Thorne, Rancho Santa Ana Botanic Garden, Claremont, California, with whom R. D. discussed the phylogenetic conclusions, and with P. H. Raven, who has given information on current work on *Roridula*. A. E. van Wyk would like to acknowledge the generosity and help received from many correspondents consulted on aspects of material incorporated in the text, in particular: P. Baas, B. A. Bohm, J. Forrester, S. A. Graham, W. J. Hayden, S. R. Jensen, N. R. Lersten, T. K. Lowrey, B. J. Nielsen, T. Patterson, P. H. Raven, H. Tobe, and G. Turner. Many thanks also to E. du Plessis and D. J. van Rensburg for technical assistance and improvements to the text, as well as to J. de Jager for the care with which she typed the manuscript. It was a great privilege to work in close cooperation with R. Dahlgren. I wish to thank him most sincerely for his encouragement, advice, and scholarly criticism.

[2] Dr. Rolf Dahlgren died tragically in an automobile accident in Sweden on February 14, 1987.

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cette région). Les Androstachydacées ne sont plus reconnues en tant que famille distincte; certaines de leurs caracteristiques permettent de les inclure dans les Euphorbiacées. Les Achariacées ont de traits en commun avec des familles des Violales à ovaires hypogènes (en particulier les Flacourtiacées et Passifloracées) et epigènes (notamment les Cucurbitacées). Les Myrothamnacées ressemblent fortement aux Hamamelidacées et aux Cercidiphyllacées; elles peuvent être classées avec les Hamamelidales. De même les Geissolomatacées, famille monotypique, ont de nombreux caractères hamamelidéen et devraient être comprises dans cet ordre ou dans un ordre unifamilial adjacent. Les Bruniacées et les Grubbiacées sont anatomiquement similaires à ces deux familles-ci, mais possèdent des ovules unitegmiques et des nucelles composées de peu de cellules, ce qui les apparente aux Ericales. On devrait peut-être alors les traiter dans les Bruniales. Les Greyiacées sont considerées comme membres du groupe des Cunoniales–Saxifragales et sont peut-être plus proches des Francoacées. Les Hétéropyxidacées représentent une famille myrtalienne distincte ayant des caractères un commun avec les Myrtacées (cavités secrétoires, pollens) et les Lythracées (anatomie ligneuse) mais elles diffèrent de ces deux familles au niveau embryologique. Les Oliniacées, Penaeacées, et Rhynchocalycacées sont des petites familles très proches les unes des autres qui, au sein des Myrtales, ressemblent les plus aux Alzateacées, Crypteroniacées, et Memecylacées, mais également aux Lythracées. Les Melianthacées appartiennent aux Sapindales et ont des points communs avec les Sapindacées et Anacardiacées. Les Ptaeroxylacées sont des Rutales au sens strict et ont des affinités avec les Rutacées et Cneoracées, tandis que les Aitoniacées xerophytes, qui sont adaptées à l'ornithophilie et l'anémochorie, devraient être incluses dans les Meliacées. Les Roridulacées et les Stilbacées sont vues comme membres des Scrophulariales (Lamiales comprises) et possèdent des caractères primitifs dans cet ordre. De nouvelles données embryologiques permettent de résoudre la question controversée concernant les relations des Retziacées; elles sont classées parmi les Stilbacées, Scrophulariacées, et Buddlejacées dans les Scrophulariales. Les Lanariacées deviennent une nouvelle famille de façon à accomoder *Lanaria*, un genre morphologiquement isolé des Asparagales; tandis que nous proposons de traiter *Walleria*, avec ses graines spécialisées, dans les Tecophilaeacées (Asparagales) comme une nouvelle sous-famille, les Wallerioïdées. Les auteurs considèrent que les Eriospermacées, dont la structure des graines est unique chez les monocotylédones, forment une famille distincte et isolée dans les Aspargales, mais leurs voisins les plus proches restent incertains.

Eight families—in the system accepted here—are endemic (Bruniaceae with the exception of one species) to the Cape floristic region, viz. Geissolomataceae, Bruniaceae, Grubbiaceae, Penaeaceae, Roridulaceae, Retziaceae, Stilbaceae, and Lanariaceae. Four of these—Geissolomataceae, Grubbiaceae, Roridulaceae, and Lanariaceae—are unigeneric, with 1–3 species each; whereas Bruniaceae contain 12, Penaeaceae 7, and Stilbaceae 5 genera. All these families are concentrated in the mountain ranges mainly in the southwestern Cape and grow in "fynbos" vegetation, a sclerophyllous, generally low scrub rich in species. The substrate is generally sand-weathered from sandstone rock, or on the rock itself, of the Table Mountain Group of the Cape Supergroup (previously known as the Table Mountain Series of the Cape System).

There are few families endemic to southern Africa outside the Cape Region. Only three small but well-defined families, Achariaceae (with three monotypic genera), Greyiaceae, and Rhynchocalycaceae (each with one genus), seem to be strictly confined to this most southernly tip of the large Palaeotropic floristic region. Myrothamnaceae, Heteropyxidaceae, Oliniaceae, and Eriospermaceae, each with one genus only, as well as Melianthaceae with two genera, are confined to Africa (Myrothamnaceae also in Madagascar) with the main center of diversity in the southern part of the continent. Ptaeroxylaceae, with two genera, have one monotypic genus on the African mainland and one genus with ca. seven species on Madagascar. The poorly circumscribed Montiniaceae comprises two genera on the African mainland, i.e., *Montinia* Thunb. in southern Africa and *Grevea* Baill. in Central Africa, and with further members (*Grevea*, *Kaliphora* Hook. fil., and perhaps *Melanophylla* Baker) on Madagascar. This family will *not* be included in the present discussion, nor will we comment on Neuradaceae, with *Grielum* L. in southern Africa and two more genera in Namibia and North Africa, respectively. *Nymania* S. O. Lindb., with one species restricted to the Cape Province and Namibia, is sometimes placed in the monotypic Aitoniaceae. In addition, the affinities of *Walleria* Kirk, ranging from the Cape Province to central Africa, will be discussed. In this connection the relationships of the unigeneric Cyanastraceae, found mainly in tropical Africa, will be evaluated.

Evidence from various sources is considered in evaluating the closest relationships of the following families enumerated in due order according to Dahlgren (1983). The authors of the family

accounts are given in parentheses; R.D. = (R. Dahlgren); A.E.v.W. = (A. E. van Wyk).

(1) Androstachydaceae (A.E.v.W.)
(2) Achariaceae (A.E.v.W.)
(3) Myrothamnaceae (R.D.)
(4) Geissolomataceae (R.D.)
(5) Bruniaceae (R.D.)
(6) Grubbiaceae (R.D.)
(7) Greyiaceae (A.E.v.W.)
(8) Heteropyxidaceae (A.E.v.W.)
(9) Oliniaceae (A.E.v.W.)
(10) Penaeaceae (R.D.)
(11) Rhynchocalycaceae (A.E.v.W.)
(12) Melianthaceae (A.E.v.W.)
(13) Ptaeroxylaceae (A.E.v.W.)
(14) Aitoniaceae (A.E.v.W.)
(15) Roridulaceae (R.D.)
(16) Retziaceae (R.D.)
(17) Stilbaceae (R.D.)
(18) Lanariaceae (R.D.)
(19) Tecophilaeaceae subfam. Wallerioideae Dahlgren (R.D.)
(20) Cyanastraceae (R.D.)
(21) Eriospermaceae (R.D.)

Each family treatment will include the following headings, where applicable: 1) a formal description of the family as circumscribed here; 2) general information on number of genera and species, and of distribution; 3) account of the treatment of the group in earlier and current literature; 4) further information, if needed, on details in macromorphology; 5) anatomy, if relevant for consideration of relationships; 6) pollen morphology; 7) embryology and seed structure; 8) chromosome numbers; 9) phytochemistry; 10) fungal or animal parasites and other biological aspects; and 11) conclusions regarding the phylogenetic relationships of the group and its appropriate taxonomic treatment, in the view of the author.

Some data are new and not yet published elsewhere, but much of the information from previous literature is included to give a reasonably complete picture of the group and to create a basis for the discussion of possible phylogenetic relationships. The myrtalean families have recently been the subject of intensive study [Ann. Missouri Bot. Gard. 71(4)], but new information is given here on the unigeneric African families. Relatively little is known about the family Stilbaceae, which are being studied in South Africa (J. Rourke); its position in Scrophulariales (incl. Lamiales) is widely accepted, although its relationships within the order and its incorporation in Verbenaceae, not supported here, require investigation.

Re-evaluation of relationships, and thus of taxonomic position, of individual genera must be made regularly, especially in rich floras where information may be incomplete. *Oftia* Adans. and *Empleuridium* Sond. & Harv. can be mentioned as examples. *Oftia* was earlier treated in the Myoporaceae, but it was shown by Dahlgren & Rao (1971) to be a member of Scrophulariaceae. In fact, it was proven to be quite similar to *Teedia* Rudophi, another South African genus. Goldblatt et al. (1985) have shown that *Empleuridium* is a member of Celastraceae and not Rutaceae, to which it had previously been referred. Its needlelike leaves are unusual for Celastraceae. Another genus in need of re-evaluation is *Lanaria* Ait., which is here placed in a separate family of Asparagales. Greyiaceae, often placed with Melianthaceae in Sapindales, are evaluated in the light of considerable evidence taken from various sources. The importance of all-round structural comparative studies and, on the basis thereof, conclusions on relationships is connected with the formation of a well-founded classification that should have predictive value in the sense that the placement of the groups (genera, families) should be able to act as a basis for reasonably successful guesses regarding hidden properties (chemical, structural) that may be searched for in the future.

The authors are in favor of monophyletic and well-circumscribed taxa (notably families), even though these may be relatively small, because only then can the predictive value of phylogenetic classifications be fully utilized.

Androstachydaceae Airy Shaw

Description. Dioecious, evergreen, or semideciduous trees; branchlets terete or slightly angular, articulated, pubescent. Leaves decussate, opposite, petiolate, simple, and sometimes slightly peltate (subgenus *Androstachys*) or digitately 3–7-foliate (subgenus *Archandrostachys*), entire, variously pubescent (often rufo-pilose), stipulate; stipules large and conspicuous, intrapetiolar, variously adnate to the petiole (inconspicuously so in *Androstachys johnsonii* Prain), connate and enclosing the apical bud, caducous (only *A. johnsonii*). Male inflorescence a shortly pedunculate triad of cernuous, catkinlike spikes or racemes of subsessile anthers, axillary; male

flowers each subtended by 2–5 loosely arranged bractlike structures (sometimes considered sepals), linear-lanceolate, hairy, sometimes with additional bracts subtending the pedicels ("rhacheae") of the lateral flowers (*A. rufibarbus* Airy Shaw); stamens numerous, spirally arranged on a prolonged axis; filaments very short; anthers linear, basifixed, 2-thecate, 4-sporangiate, latrorse, longitudinally dehiscent; connective apically hairy, elongated in some species (subgenus *Archandrostachys*); ovary and disc absent. Pollen grains shed as monads, yellowish and not sticky when fresh. Female flowers solitary, axillary, pedicelled, subtended by 5–6 bractlike structures (sepals?), imbricate, apparently in two series; disc and stamens absent; ovary superior, sessile, 3(–5)-locular; style elongated with three spreading, linear-lanceolate stigmatic lobes; ovules two per locule, collateral on apical-axile placentae, anatropous, epitropous with a ventral raphe, obturator present. Fruit a loculicidal and septicidal crustaceous capsule, depressed-globose, often with a dense indumentum. Seeds elliptical-globose, sometimes with a minute aril (subgenus *Archandrostachys*); testa hard and shiny, brownish; embryo straight with two collateral rounded cotyledons, chlorophyllous; endosperm abundantly present, oily.

General information. The Androstachydaceae, a family of doubtful status, consist of the genus *Androstachys* Prain with about five species, one shared between Africa and Madagascar, and the others endemic to the latter region.

The present account is based mainly on *Androstachys johnsonii* Prain, the type species of the Androstachydaceae, since material of the other species (subgenus *Archandrostachys*) was not available for study. Attention is directed particularly to whether *A. johnsonii* should be referred to a distinct family or be accommodated in the Euphorbiaceae. Remarks on its possible nearest relatives, particularly *Hyaenanche globosa* (Gaertn.) Lamb., are also presented.

Androstachys johnsonii is a dioecious evergreen or semideciduous tree confined to southeastern Africa and Madagascar. At least in southern Africa the species is gregarious, forming almost pure stands often on rocky ridges (Van Rooyen, 1978; Van Rooyen et al., 1981). It is particularly common on the relatively hot and dry stony (sandstone) slopes of the Lebombo and Soutpansberg mountain ranges. The heartwood is extremely hard, heavy (990 kg/m^3, air-dried) and very durable (Van Wyk, 1974). When burning it produces a subtle fragrance reminiscent of incense. All parts of the plant are without latex.

Treatment in the literature. Androstachys johnsonii was described by Prain (1908) and without hesitation assigned to the Euphorbiaceae. Pax & Hoffmann (1922, 1931) associated *Androstachys* with the Cape endemic *Hyaenanche globosa* (= *Toxicodendrum globosum* (Gaertn.) Pax & K. Hoffm.). The two genera constitute the subtribe Toxicodendrinae of tribe Phyllantheae, subfamily Phyllanthoideae (group Platylobeae).

Subfamilies were abandoned by Hutchinson (1969), who only recognized 40 tribes in Euphorbiaceae. *Androstachys* together with *Hyaenanche* Lamb., *Austrobuxus* Miq. (= *Longetia* Baill.), *Paradrypetes* Kuhlm., *Dissiliaria* F. Muell., and *Mischodon* Thw. are treated as members of the tribe Hyaenancheae.

On the basis of palynological evidence especially, Webster (1975) proposed a new classification of the Euphorbiaceae. He subdivided the family into five subfamilies: Phyllanthoideae s. str. and Oldfieldioideae (both formerly Phyllanthoideae and Porantheroideae), Acalyphoideae, Crotonoideae s. str., and Euphorbioideae (all three previously included in Crotonoideae s.l. and Ricinocarpoideae). Both *Androstachys* and *Hyaenanche* are placed in the Oldfieldioideae but in separate tribes. *Androstachys* and the Australian *Petalostigma* F. Muell. constitute the tribe Petalostigmateae, whereas *Hyaenanche* is placed in the monogeneric subtribe Hyaenanchinae of Hyaenancheae. The basic groups, Stenolobeae (which was dismembered by Webster) and the Platylobeae, are maintained by Airy Shaw (1983), who recognizes two subfamilies in each, whereas *Antidesma* L. is referred to a separate family, the Stilaginaceae. The latter classification was tailored particularly for the Australian flora, and *Androstachys* is not considered. For a recent review of the taxonomic history of the Euphorbiales, see Webster (1987).

Androstachydaceae was described by Airy Shaw (1965) to accommodate *A. johnsonii*. A distinct family for the species was deemed justified mainly because of its unique catkinlike male inflorescences with floral triads and the simple decussate leaves with remarkably connate intrapetiolar (also interpetiolar owing to the lateral fusion) stipules, which are caducous. Subsequently, Airy Shaw (1970) described four new species of *Androstachys* from Madagascar. Leroy (1976) created a new subgenus *Archandrostachys*

to accommodate these species, which differ from *A. johnsonii* in having digitately 3–7-foliate leaves, stipules adnate to the petiole, a minute caruncle (at least in some species), and a few other features. Despite the conspicuous vegetative differences, floral characters are almost identical in all five species (Airy Shaw, 1970).

The genus *Voatamalo*, with two species in Madagascar, was described by Bosser (1976) and considered related to *Austrobuxus* (Phyllanthoideae) from New Caledonia and the Malay peninsula. According to Bosser, the decussate leaves and intrapetiolar stipules of *Voatamalo* are similar to those of *Androstachys*. However, Bosser pointed out that it would be premature to consider *Voatamalo* a possible link between *Androstachys* and other Euphorbiaceae. In fact, *Voatamalo* lacks the peculiar male inflorescences of *Androstachys*, and a nectariferous disc is present in both male and female flowers (absent in *Androstachys*). Leroy (1976, 1978) would nevertheless seem to regard *Voatamalo* close enough to *Androstachys* for inclusion in the Androstachydaceae. In the present account, however, *Voatamalo* is considered too distantly related to *Androstachys* for inclusion in the original concept of Androstachydaceae.

Androstachydaceae is maintained as a distinct family by Airy Shaw (1973) but incorporated into Euphorbiaceae by Takhtajan (1980) and Cronquist (1981). Radcliffe-Smith (1987) also discussed the taxonomic status of Androstachydaceae and supported the latter view.

Macromorphology. In Euphorbiaceae the leaves are usually simple and alternately arranged. However, opposite leaves as in *Androstachys* are not uncommon, especially among members of the Oldfieldioideae. Intrapetiolar stipules are very rare but do occur in *Voatamalo*. The leaves of *Hyaenanche* are arranged in whorls of four with minute interpetiolar free stipules, thereby differing conspicuously from those of *Androstachys*. Occasionally the heart-shaped leaves of *Androstachys* tend to be subpeltate, a condition also known in some Euphorbiaceae (e.g., the African *Heywoodia* Sim and *Macaranga* Thou.).

The female flowers of *Androstachys* consist of a 3(–5)-locular ovary subtended by bractlike structures (sometimes described as sepals). They are typically euphorbiaceous.

The male inflorescences of *Androstachys* consist of a shortly pedunculate triad of cernuous, catkinlike spikes or racemes of subsessile anthers—a structure unknown elsewhere in the flowering plants (Airy Shaw, 1965). Each member (flower) of the triad is subtended by a group of loosely arranged bractlike appendages. The flowers are perhaps essentially naked (see Airy Shaw, 1976: 367). Male inflorescences of some members of subgenus *Archandrostachys* are more primitive than those of *A. johnsonii*, thereby allowing some evolutionary speculation. Leroy (1976) considered the components of the male inflorescence to comprise three flowers and hypothesized that the very differently arranged solitary female flowers could have been derived through reduction from a similarly branched female inflorescence. An interesting discussion of the bearing of the possible trends of inflorescence evolution in *Androstachys* on theories attempting to explain the origin of flowers in the Euphorbiaceae in particular and the angiosperms in general is presented by Leroy (1976).

Male inflorescence structure is extremely diverse in Euphorbiaceae. Stamens arranged on a column (androphore) vaguely recalling *Androstachys* occur, for example, in male flowers of *Petalostigma, Cocconerion* Baill., *Borneodendron* Airy Shaw, and *Stachystemon* Planch. Some of these staminal columns may not be homologues of the staminal axis in *Androstachys* (Airy Shaw, 1963, 1971, 1976). Taken separately, the unique structure of the male inflorescences of *Androstachys* does not provide sufficient evidence to justify its exclusion from the Euphorbiaceae. Also a hairy anther apex such as that in *Androstachys* is known in some other Euphorbiaceae, occurring for example in a less conspicuous form in *Manihot* Mill., *Mischodon, Cocconerion, Borneodendron,* and *Petalostigma.* The hairy anther apex in *Androstachys* is considered by Leroy (1976) to arise from the rudimentary sterile portion of the microsporophyll to which the also hairy, bractlike structures in the inflorescence are suspected to be homologous.

Flowers of *A. johnsonii* are most probably anemophilous, a condition also suspected by Leroy (1976). This is suggested particularly by the exposed catkinlike male inflorescences that wither soon after the release of abundant nonsticky pollen. Both male and female flowers lack nectaries. Reports that honey prepared from the flowers of *A. johnsonii* is poisonous (D. G. Steyn, 1934, 1949) should be reconsidered in view of the expected absence of nectar in the flowers. The chance of being pollinated by wind is promoted considerably by the gregarious habit of the species.

Anatomy. In a note published shortly after the formal description of *Androstachys johnsonii,* some brief comments on the anatomy of the species were presented (Anonymous, 1909). According to L. A. Boodle, the anatomy of the leaf and stem do not support an affinity with Buxaceae but are quite concordant with Euphorbiaceae. However, Metcalfe & Chalk (1950) remarked that the wood anatomy of *Androstachys* does not support its inclusion in Euphorbiaceae. Airy Shaw (1973) seemed to consider the anatomical characters of *Androstachys* as major evidence against a close affinity with Euphorbiaceae. For a reassessment of anatomical characters, we examined bark, wood, leaf, and stem samples of *A. johnsonii.*

An outstanding anatomical feature of *Androstachys johnsonii* leaves is the abundant presence of long fiberlike sclereids. The sclereids are occasionally branched and obviously develop from the vertical transcurrent bundle sheath extensions. They are mainly associated with the vascular bundles (even the smallest ones), with occasional deviating sclereids spreading mainly just below the adaxial and abaxial epidermis. The areoles are well developed, and no free-ending veinlets were observed. Fiberlike leaf sclereids are widespread in Euphorbiaceae (Solereder, 1908; Metcalfe & Chalk, 1950; Rao & Das, 1979).

Most of the adaxial epidermal cells of *Androstachys johnsonii* have mucilaginous inner cell walls. This is also a noteworthy anatomical feature of the epidermis in many Euphorbiaceae (Solereder, 1908; Metcalfe & Chalk, 1950; Raju & Rao, 1977). The leaves of *A. johnsonii* are hypostomatic and the stomata are concealed by a dense indumentum of long, curly, bicompartmented simple trichomes. The basal compartment of the trichomes is very small and the thick septum separating it from the long terminal portion occurs just above the cuticular surface. The base of the trichome is narrowed into a peglike foot inserted between three or more cells of the epidermis. In surface view the epidermal cells are polygonal with more or less straight anticlinal walls. In one sample the anticlinal walls of the lower epidermis displayed conspicuous knoblike thickenings. Rather similar thickenings were recorded by Raju & Rao (1977) in some species of Euphorbiaceae.

Interpretation of the morphology of the stomatal apparatus was made rather difficult by the presence of the trichomes, which had to be scraped off to reveal the cuticular surface. The stomata are interpreted as essentially paracytic, with the subsidiary cells often not meeting over the guard cell poles ("brachyparasitic" of some authors). Nearly all the subsidiary cells are subdivided by one or two relatively thin walls perpendicular to the long axis of the guard cells. Stomata in the Euphorbiaceae are usually brachyparacytic and the leaves either amphistomatic or hypostomatic (Solereder, 1908; Metcalfe & Chalk, 1950; Raju & Rao, 1977). No reference to a stomatal type similar to that of *Androstachys johnsonii* (perhaps best designated as "complex paracytic") could be traced for a member of the Euphorbiaceae. Brachyparacytic stomata, however, are common throughout subfamily Oldfieldioideae (W. J. Hayden, pers. comm.). Some stomata with both subsidiary cells subdivided vaguely resemble the cyclocytic stomata of the Buxaceae.

Three leaf traces enter the petiole. Transverse sections through the mid part of the petiole exhibit a more or less closed vascular cylinder with the adaxial part strongly invaginated, resulting in a complex crescentic pattern. Accessory bundles are lacking. This vascular pattern indicates a strong affinity to the vascular patterns known in the Euphorbiaceae (Dehay, 1935; Metcalfe & Chalk, 1950).

The stem anatomy does not supply any characters of particular taxonomic significance. The periderm arises in the outer part of the cortex to the inside of a subepidermal hypodermis composed of about three layers of thick-walled cells. A continuous ring of extraxylary fibers transversed by sclerosed ray parenchyma cells is present. These features were also reported by Boodle in Anonymous (1909).

The wood anatomy of *Androstachys johnsonii* is outstanding and, in its combination of characters, is unlike any known member of the Euphorbiaceae, in particular the subfamily Phyllanthoideae s.l. This was pointed out by Metcalfe & Chalk (1950), and we confirm their observations. Noteworthy features include wood diffuse-porous with distinct growth rings, pores nearly always solitary, perforation plates exclusively simple, intervascular pitting alternate, fibers not septate and with pits conspicuously bordered (fiber tracheids), inner pit apertures included, axial parenchyma virtually absent (limited to a few scattered tanniniferous and starch-containing cells in the vicinity of some vessels), rays exclusively uniseriate and homogeneous (heterogeneous, according to Metcalfe & Chalk, 1950), prismatic crystals sparingly present in sclerosed, chambered crystalliferous chains of variable length,

heartwood vessels usually with dark-colored deposits, and the sapwood very narrow. Taken separately, most of these characters are present among members of Euphorbiaceae. It is the particular combination of characters that renders the wood of *A. johnsonii* so unusual.

A study of mature bark samples revealed an interesting anatomical structure. The inner bark is composed of regularly alternating, more or less concentric bands of hard and soft bast. The bands of hard bast are usually 8–12 cell layers wide and are composed of densely packed cylindrical phloem fibers and sclerosed, chambered crystalliferous strands with a single prismatic crystal in each chamber. The fibers are relatively sparse and confined mainly to the inner and outer layers of a band. Sclerosed ray parenchyma cells are found where the rays traverse a band of hard bast. Expansion tissue was absent in the samples studied. The rhytidome is well developed with conspicuous longitudinal fissures. It consists of several interconnected layers of successive periderms cutting off more or less concentric layers of inner bark. These layers of dead inner bark are fairly resistant to decay and alternate with multilayered bands of phellem, which is not stratified and is composed of cells with relatively thin, unlignified walls. Weathering processes cause the older layers of phellem to crumble with the resultant sloughing of irregular pieces of rhytidome. No distinct phelloderm is present.

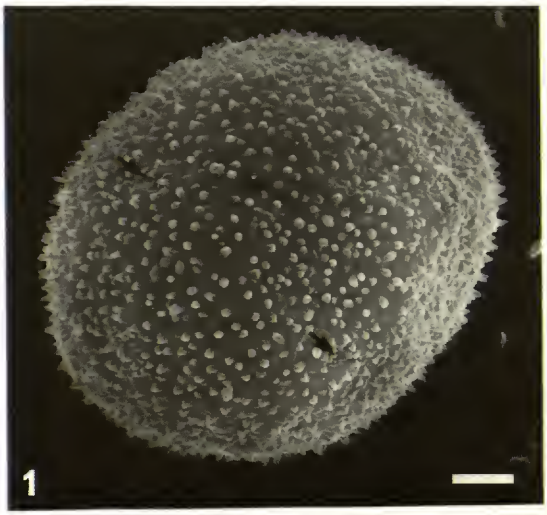
Information on the mature bark structure in Euphorbiaceae is scanty. However, a regular stratification of the inner bark appears to be very rare in the family (Thorenaar, 1926; Metcalfe & Chalk, 1950; Roth, 1981). Roth (1981) found a regular stratified inner bark only in *Piranhea longipedunculata* Jabl. The hard bast in the latter species is composed of sclereids only. Metcalfe & Chalk (1950) noted, however, that in terms of wood anatomy *Piranhea* Baill. is somewhat anomalous in Euphorbiaceae. Present evidence suggests that the mature bark structure of *A. johnsonii* is unusual for Euphorbiaceae.

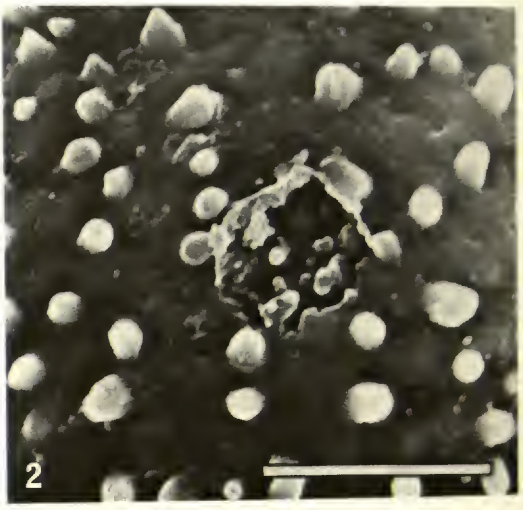
Alleged affinities between *Androstachys* and *Hyaenanche* are not at all supported by the comparative anatomy of the leaf and stem. Anatomical descriptions for *Hyaenanche* (Gaucher, 1902; Dehay, 1935) were supplemented by observations made during the present study. Leaf sclereids, mucilaginous epidermal cells, and complex paracytic stomata are absent in *Hyaenanche*. An open vascular arc with the ends slightly incurved is present in the petiole of *Hyaenanche*. It is replaced by a more complex vascular strand in *Androstachys*. Venation patterns are completely different in the two genera. Areolation is poorly developed in *Hyaenanche*, and branched veinlets are conspicuously present.

Since writing the preceding anatomical notes, detailed descriptions of the leaf anatomy of *A. johnsonii* have been provided by Alvin (1987) and Alvin & Rao (1987).

Pollen morphology. Euphorbiaceae are a distinctly europalynous family palynologically (Erdtman, 1952), and this may limit the taxonomic value of pollen features. Pollen morphology has nevertheless proved to be quite useful for the elucidation of relationships within the family (Punt, 1962; Köhler, 1965; Webster, 1975). Comparisons must be made with care, however, because different pollen types may occur in the same genus, and quite often different genera possess the same pollen type (Punt, 1962). Punt classifies the pollen grains of *Androstachys johnsonii* under the *Stachystemon* type, characterized, among other features, by being periporate or inaperturate and echinate. Pollen grains of *A. johnsonii* are more or less spheroidal, and he considers them inaperturate. Other genera with grains classified as the *Stachystemon* type mainly belong to the biovulate Stenolobeae (the subfamily Porantheroideae of some authors). *Androstachys johnsonii* seems somewhat anomalous in this grouping because the pollen grains of all the other genera associated with it are periporate. Punt (1962) stressed the fact that the so-called Croton pattern is frequently encountered among genera of the Crotonoideae, many of which also have inaperturate pollen grains. No Croton pattern is present in grains of *A. johnsonii*. Despite some similarity to grains of a few Crotonoideae lacking the Croton pattern, he retains *Androstachys* under the Phyllanthoideae without questioning its taxonomic placement.

Köhler (1965) investigated the pollen morphology of many biovulate members of the Euphorbiaceae. Grains of *Androstachys johnsonii* are classified in a group of their own, viz. the *Androstachys* type, which Köhler described as ± pantoporate (= periporate) or perhaps dizonoporate, with 14–18 inconspicuous pores (without costae) per grain. Erdtman (1952) also described the grains of *A. johnsonii* (the same sample as studied by Köhler!) as "oligoforate" = provided with 12 or fewer pores, which he noted are faintly defined and covered with granulate membranes. Köhler suggested that *Androstachys* should, on pollen morphological grounds, be retained in the





FIGURES 1, 2. Scanning electron micrographs of *Androstachys johnsonii* pollen (acetolyzed).—1. Surface features of grain. Note lack of distinct pores but presence of "cryptic" pores (some arrowed).—2. Enlargement of "pore" covered by a granular membrane. Scale line = 5 μm. Material, *Van Wyk 5887* (PRU).

Toxicodendrinae together with *Hyaenanche,* although he appreciated its isolated taxonomic position. He also considered *Petalostigma* (of the monogeneric *Petalostigmatinae*) somewhat related to the former subtribe.

The discrepancy between the pollen descriptions of *Androstachys* supplied by Erdtman (1952) and Köhler (1965) on the one hand (grains aperturate) and Punt (1962) on the other hand (grains inaperturate) has led to a reinvestigation of several pollen samples. Not to add further to the confusion, acetolyzed grains were studied very carefully with both light and scanning electron microscope. Nearly all the investigated grains appeared inaperturate, thereby confirming the observations by Punt (Fig. 1). Rarely were grains with up to two "pores" seen under the SEM. These "pores" seem to represent weak spots in the exine that were torn during preparation of the pollen (Fig. 2). There may be more of these cryptic "pores" present. *Androstachys johnsonii* appears to be the only known member of the Phyllanthoideae with inaperturate pollen grains. However, the latter statement depends on the interpretation given to the "weak spots" in the pollen wall. If these are considered apertures, the grains could alternatively be interpreted as aperturate (thereby confirming the descriptions by Erdtman and Köhler). For palynological reasons there is not much evidence in favor of a close affinity between *Androstachys* and *Hyaenanche.* Pollen grains of *Hyaenanche* are 6–9-colporate with a spinuliferous sexine. The apertures are situated in the equatorial plane (zonotreme) (Erdtman, 1952; Punt, 1962; Köhler, 1965).

See Punt (1987) for a recent discussion of Webster's (1975) subdivision of the Euphorbiaceae in relation to pollen morphology.

Embryology and seed. Each locule of the ovary contains two collateral ovules attached to apical-axile placentae (a distinguishing character of Phyllanthoideae s.l.). The ovules are epitropous with a ventral raphe. Some authors have claimed a superficial resemblance between *Androstachys* and Buxaceae. This resemblance is of little systematic significance because Buxaceae are characterized by apotropous ovules with a dorsal raphe (Cronquist, 1981—but the validity of this statement is in need of critical study because Corner (1976) described and illustrated the ovules of *Sarcococca zeylanica* Baill. as epitropous with a ventral raphe). An obturator, which is so characteristic of Euphorbiaceae, is present in *A. johnsonii* (most probably also in the other species of the genus). In some ovules the nucellus protrudes slightly from the micropyle to ensure close contact with the obturator. The general ovary structure of *Androstachys* fully supports its placement in Euphorbiaceae.

We also examined the structure and development of the seed coat in *Androstachys johnsonii,* hitherto undescribed. During seed development both integuments become thicker owing mainly to an increase in the size of the outer epidermal and mesophyll cells (notably the ca.

four cell layers of the outer integument). The seed coat is clearly nonmultiplicative. During the early stages of seed development the inner integument remains thin and insignificant. About 80% of the width of the seed coat is occupied by the outer integument. Half the width of the latter consists of the outer epidermal layer. Outer epidermal cells of the outer integument enlarge and become radially elongated. Brownish colored substances are deposited in these cells, which, like the rest of the cells in the outer integument, remain thin-walled and unlignified. In the mature seed the cells of the outer integument (testa) are more or less collapsed, with only the now irregular layer of darkly colored outer epidermal cells fairly prominent.

It was difficult to establish whether the main mechanical layer of the seed coat develops from the inner epidermis of the outer integument or from the outer epidermis of the inner integument. The latter interpretation seems the most likely and has been adopted, hence the seeds of *Androstachys johnsonii* are considered exotegmic. The mechanical tissue is composed of a uniserial layer of long, slightly laterally compressed fibers with thick, lignified walls. In surface view the fibers display a regular longitudinal arrangement and, in transverse section, sometimes give the appearance of a short palisade. The mesophyll cells of the inner integument remain thin-walled and unlignified but are eventually more or less crushed in the mature tegmen. The inner epidermis is persistent and composed of small, thick-walled (slightly lignified) cells with numerous conspicuous simple pits present in the anticlinal walls. The latter layer is distinctive in surface view and is similar to the pitted exotegmen illustrated by Corner (1976) for *Sarcococca zeylanica* (Buxaceae) and *Bischofia javanica* Blume (Euphorbiaceae, sometimes in Bischofiaceae).

Exotegmic seeds with tangentially elongated fibers that are usually longitudinal on the seed are frequently encountered in part of the Phyllanthoideae s.l. (Corner, 1976). Evidence from basic seed coat structure therefore strongly supports the placement of *Androstachys* in Euphorbiaceae. In fact, it corresponds so closely to the seed coat structure in some members of the Phyllanthoideae that it is tempting to consider this evidence decisive for retaining *A. johnsonii* in the Euphorbiaceae. Moreover, the mature seeds of *A. johnsonii* contain oily endosperm, which is the prevailing state in Euphorbiaceae. The cotyledons are flat, rather fleshy, and much broader than the relatively short radicle. This would confirm its placement in the Platylobeae, one of the major groups into which Euphorbiaceae can be subdivided (for a recent opinion on the validity of the basic division of the family into the Stenolobeae and Platylobeae, see Airy Shaw, 1983). Chlorophyll is present in the embryo of *A. johnsonii* but absent from the endosperm. Both chlorophyllous and achlorophyllous embryos are known in the Euphorbiaceae (Yakovlev & Zhukova, 1980). Chlorophyllous embryos are found more or less regularly in the seeds of certain families and orders, thereby rendering this feature taxonomically significant (Yakovlev & Zhukova, 1980; Dahlgren, 1980b). A survey of the presence or absence of chlorophyll in embryos of the diverse Euphorbiaceae may be useful for establishing intrafamilial affinities. Embryos of *Hyaenanche globosa* have also been described as green (Pax & Hoffmann, 1922), which we can confirm from our own examination of live material.

The seeds of *Androstachys johnsonii* also lack postchalazal vascular bundles and a caruncle. It has been claimed that carunculate seeds are confined to the Crotonoideae, perhaps with the possible exception of the Phyllanthoid genera *Hyaenanche* and *Petalostigma* (Corner, 1976). Seeds of *Androstachys* subgenus *Archandrostachys* are also described as being minutely carunculate (Airy Shaw, 1970; Leroy, 1976). A very small caruncle is present in mature seeds of *Hyaenanche globosa,* thus confirming previous claims as to its presence in this species (e.g., Pax & Hoffmann, 1922, 1931). In this respect *Hyaenanche* is considered anomalous in Phyllanthoideae (cf. doubts raised by Corner, 1976: 131, 138).

Chromosome number. Apparently not yet recorded.

Phytochemistry. Information on the chemistry of *Androstachys* and putative allies is far too limited for its taxonomic significance to be assessed. Oliveira (1971) listed *A. johnsonii* in a chemical analysis of tropical woods, but the attributes investigated are not taxonomically relevant. The findings of Pegel et al. (1971) deserve more attention. They found that the major heartwood diterpene of *A. johnsonii* presents the first instance of a C-12 oxygenated beyerane-type diterpene, and the possible existence of a new type of diterpene skeleton is suggested. The "Aluminon" test for aluminum accumulators is negative for *A. johnsonii.* Concerning a possible af-

finity between *Androstachys* and *Hyaenanche,* it should be noted that the seeds of *H. globosa* are extremely toxic. The main toxic principle is known as hyaenanchin; it is neither an alkaloid nor a glucoside, but probably a dilactone. Traces of the compound are present in the leaves and stems. It has an action about a quarter of the strength of strychnine (D. G. Steyn, 1949; Watt & Breyer-Brandwijk, 1962). With the exception of reports, mentioned above, that honey produced from flowers of *A. johnsonii* is poisonous (which may be erroneous), this species does not appear to contain notable toxic principles. In fact, the leaves are browsed without ill effect by stock and wild animals, and the fruits and seeds are eaten by animals such as duiker, squirrels, and birds (Palmer & Pitman, 1972; Van Wyk, 1974).

Conclusions and relationships. Airy Shaw (1965) remarked that the anatomy of *Androstachys johnsonii* apparently resembles in many respects that of *Microdesmis* Hook. f. [sometimes referred to the Pandaceae, but retained by Corner (1976) in Euphorbiaceae, Phyllanthoideae]. We are unable to confirm this remark, but it is clear that at least on morphological grounds *Microdesmis* and *A. johnsonii* are not at all closely related. *Microdesmis* is quite different in its pseudopinnate, distichous arrangement of leaves on lateral shoots of limited growth, toothed leaf margins, stipules free and not intrapetiolar, flowers with calyx and corolla, stamens 5 or 5 + 5, locules with solitary ovules, and the fruit a drupe. Most of the latter features also apply to the other two genera of the Pandaceae, *Galearia* Zoll. & Mor. and *Panda* Pierre (Forman, 1966). In leaf and stem (Metcalfe, 1966) as well as in wood anatomy (Parameswaran & Metcalfe, 1966) *Galearia* and *Panda* do not show a close affinity with *Androstachys.* The seed coat structure of *Microdesmis* vaguely resembles that of *Androstachys,* but unfortunately the descriptions provided by Vaughan & Rest (1969) do not clearly indicate whether elements belong to the testa or the tegmen. Conspicuous stone cell zones render the seed coats of *Panda* and *Galearia* (Vaughan & Rest, 1969) rather different from those of *Androstachys* and *Microdesmis.* A possible affinity between *Androstachys* and Buxaceae previously referred to is refuted by the presence of an exomesotestal seed coat in the latter family (Corner, 1976).

Androstachys (*A. johnsonii* in particular) has various features in support of a placement in the Euphorbiaceae. These include attributes pertaining to the general morphology of the ovary and the ovules, various seed characters—particularly the structure of the seed coat—and anatomical characters of the leaf, stem, and petiole. Evidence does not favor a close affinity with Pandaceae and Buxaceae. Within the Euphorbiaceae it occupies a very isolated position suggested by its unusual vegetative morphology, male inflorescences, bark and wood anatomy, stomatal type, and pollen morphology. A first priority should be to ascertain whether these distinctive features are present also in the other members of the genus (subgenus *Archandrostachys*). Only then could one attempt to speculate with some confidence on the intrafamilial position of the genus. What is clear, however, is that *Hyaenanche,* with which it was hitherto often associated, does not appear to be closely related to *Androstachys.* Neither does *Androstachys* show a close affinity to *Petalostigma,* which according to Airy Shaw (1976) is perhaps closest to *Pseudolachnostylis* Pax. Treatment of *Androstachys* in a tribe of its own under the subfamily Oldfieldioideae may be the answer, but such a decision must be left to an expert on the Euphorbiaceae.

To recognize a distinct family Androstachydaceae does not seem to be warranted at this stage. Euphorbiaceae is a large and complex family of diverse composition. Indications are that it is composed of genera derived from various different stocks, hence its heterogeneous composition. Although much desired, a satisfactory subdivision of the family has not yet been accomplished, and to uphold Androstachydaceae would be to deny the existence of other similarly distinctive groups within the family. However, the recognition of many relatively small but more natural segregate families could be a future solution. Among them will most probably be the Androstachydaceae. For the present *Androstachys* is retained in the Euphorbiaceae.

According to Airy Shaw (1970), the Madagascar material of *Androstachys johnsonii* agrees perfectly with that from Africa (no male flowers were seen). Leroy (1976) is less certain about this and refers to the Madagascar material as *A.* cf. *johnsonii.* That the material from the two regions is slightly different is also maintained by Leroy (1978). Whatever the case may be, the distribution of *Androstachys* is an interesting one from a phytogeographical point of view. However, a detailed discussion of the matter would be outside the scope of the present paper. Suffice it to say that *Androstachys* is considered a Gondwana relic. Its long history and inherent powers of sur-

vival are today also reflected in its isolated taxonomic position. Therefore it is not suprising that suggested allies are usually monotypic or small, taxonomically well-defined genera widely scattered on mainly eastern Gondwana fragments.

Achariaceae Harms in Engler & Prantl

Description. Herbaceous glabrous climbers twining to the left (*Ceratiosicyos* Nees), subherbaceous pubescent shrublets up to 0.5 m high (*Acharia* Thunb.) or acaulescent glabrous herbs (*Guthriea* H. Bol.); plants monoecious, tardily deciduous to deciduous (*Acharia* and *Guthriea*) or essentially rhizocarpic (*Ceratiosicyos*). Leaves alternate, simple, petiolate, palmately lobed (*Ceratiosicyos* and *Acharia*) or unlobed (*Guthriea*), serrate or crenate, chartaceous or subchartaceous, exstipulate. Inflorescence a raceme or flowers solitary, axillary, male often maturing before female flowers. Flowers pedicellate, unisexual and without rudiments of the opposite sex, actinomorphic, 3–5-merous, sympetalous, hypogynous; glands 3–5, antipetalous, fleshy, linear, ovate, obovate or fusiform, ca. 1–2 mm long, yellowish to bright orange, inserted on the receptacle at the base of the corolla tube. Sepals usually linear, shorter than, and sometimes adnate to, the corolla tube. Corolla greenish white, campanulate (*Acharia* and *Guthriea*) or with the lobes cohering by marginal cilia, thus appearing urceolate (*Ceratiosicyos*). Male flowers with the stamens in one cycle, as many as, and alternate with, the corolla lobes, inserted on the receptacle or epipetalous (*Guthriea* only), straight in bud; filaments free; anthers with a broad connective, free in *Acharia* and *Guthriea* but with the lateral margins tightly cohering in *Ceratiosicyos,* basifixed to almost dorsifixed in *Guthriea,* nonversatile, 2-thecous, 4-sporangiate, introrse, longitudinally dehiscent, thecae fringed with peculiar swollen trichomes in *Acharia* and *Guthriea,* but in *Ceratiosicyos* confined to the free apical margin of the coherent anthers. Pollen grains shed as monads, bright yellow and clumping together when fresh (only observed in *Ceratiosicyos*), large quantities being retained within the narrow channel formed by the coherent anthers in *Ceratiosicyos.* Female flowers with the ovary superior, shortly stalked in *Ceratiosicyos* and *Acharia,* inner and outer surface densely pubescent in *Acharia,* 1-locular, with few to many anatropous ovules on 3–5 parietal placentae; style 3–5 lobed with additional divisions in *Ceratiosicyos,* lobes tubular with an apical opening in *Guthriea.* Fruit a 3–5-valved capsule. Seeds subglobose, exarillate; testa pitted or tubercled, raphe expanded (ridged) in *Acharia* and *Guthriea*; embryo straight with ovate cotyledons; endosperm oily, abundantly present.

General information. A family comprising three monotypic genera of diverse habit and habitat: *Acharia tragodes* Thunb., a rare sparsely branched semiwoody shrublet of valley bushveld, centered in the eastern Cape; *Ceratiosicyos laevis* (Thunb.) A. Meeuse, a herbaceous nontendriliferous twiner from forest margins particularly along the eastern escarpment; and *Guthriea capensis* H. Bol., a rosette plant with underground rootstock occurring in open grassland on the southern Drakensberg and high mountains (during winter often covered in snow) of the Karoo. The most recent taxonomic revision is by Killick (1976a). Until recently very little evidence besides that from macromorphology was available for the family. Moreover, many existing descriptions and illustrations of members of Achariaceae contain numerous errors. An in-depth study of the family (in collaboration with E. du Plessis) has been initiated, and some of the more significant findings to date will be briefly mentioned in this account.

Treatment in the literature. Achariaceae have been widely regarded as related to Passifloraceae, with which they are associated in all modern systems of classification. The family has sometimes been included as a separate tribe Acharieae in Passifloraceae (e.g., Bentham & Hooker, 1867; Harms, 1893a, 1893b). Achariaceae were first recognized by Harms (1897), largely because of the distinctly sympetalous corollas and lack of a corona and aril. Harms (1925) noted that the broad connective of the anthers is reminiscent of some Cucurbitaceae. The cucurbitaceous habit of *Ceratiosicyos* led Hutchinson (1967) to speculate that Achariaceae may represent a link between Passifloraceae and Cucurbitaceae.

Macromorphology. Stipules are wanting in Achariaceae, thereby confirming the family descriptions of Hutchinson (1959, 1967) but not that of Cronquist (1981), who considers the family stipulate. Passifloraceae and Flacourtiaceae are usually stipulate (sometimes small and caducous), whereas Cucurbitaceae are exstipulate.

Achariaceae are monoecious and agree with Cucurbitaceae in the sympetalous campanulate corollas. Sympetaly is a feature not often associated with unisexual flowers, except in Cucur-

bitaceae and some Euphorbiaceae (Hutchinson, 1969).

Flowers in Achariaceae are hypogynous, suggesting perhaps a closer affinity with families such as Passifloraceae, Turneraceae, and Flacourtiaceae than with the epigynous Cucurbitaceae. Serological evidence also supports the distinction between hypogynous and epigynous "Parietales" (Kolbe & John, 1979). Unfortunately Achariaceae were not included in the latter study. Anther morphology of Achariaceae is nonetheless strongly reminiscent of some Cucurbitaceae. Peculiar swollen trichomes fringe the thecae in *Acharia* and *Guthriea* and have now also been discovered apically on the anthers of *Ceratiosicyos*. These trichomes recall similar structures on the anthers of various Cucurbitaceae (e.g., Knuth, 1908; Chakravarty, 1958; Jeffrey, 1962, fig. 3(4), p. 365). An affinity with Cucurbitaceae is also strengthened by the broad connective and particularly the coherence of the anthers in *Ceratiosicyos* (the floral morphology of the latter suggests a very interesting pollination biology). Male flowers of *Guthriea* have the stamens adnate to the corolla tube and are superficially rather similar to those of Cucurbitaceae, particularly members of the tribe Melothrieae. Among Cucurbitaceae the primitive Zanonioideae differs from Achariaceae in its 2–3-locular ovaries and does not appear to constitute a link between Achariaceae and the rest of the Cucurbitaceae.

Anatomy. Although leaf, stem, and root anatomy of Achariaceae have been studied in detail, anatomical evidence is not very helpful in the elucidation of interfamily relationships. Anatomically, the family is diverse—a reflection of the markedly different habits of the three genera. Noteworthy is the lack of internal phloem, which is such a characteristic feature of most Cucurbitaceae (except the Zanonioideae, cf. Jeffrey, 1980).

Pollen morphology. Pollen morphology supports the isolated position of the three genera. Grains are tricolporate with a reticulate to smooth sexine (Erdtman, 1952). According to Erdtman, more or less similar grains occur in Cucurbitaceae and Passifloraceae.

Embryology and seed. Embryological evidence is still very scanty. The ovules in *Ceratiosicyos* and *Acharia* are anatropous, bitegmic, and crassinucellar with a prominent nucellar beak. A beaked nucellus is characteristic for Cucurbitaceae (e.g., Singh, 1953; D. Singh, 1970; Singh & Dathan, 1973, 1974) but apparently not for Passifloraceae (B. Singh, 1970). It is also present in some Flacourtiaceae (e.g., Van Heel, 1973, 1974). Copious oily endosperm is present in the seeds of Achariaceae, Passifloraceae, and Flacourtiaceae. Endosperm is wanting or nearly so in Cucurbitaceae.

Seed coat development and structure in *Ceratiosicyos* are quite unlike those of the Cucurbitaceae. Both integuments partake in seed coat formation, and the seeds are clearly exotegmic, thereby resembling the tegmic seeds of Passifloraceae and Flacourtiaceae (B. Singh, 1970; Corner, 1976; Van Heel, 1977). Seeds of Cucurbitaceae have an exotestal seed coat derived entirely from the outer epidermis of the outer integument (D. Singh, 1970; Corner, 1976).

Chromosome number. Chromosome number in *Ceratiosicyos* is $2n = \pm 20$ (T. K. Lowrey, pers. comm.). More or less similar counts are known in Passifloraceae, Flacourtiaceae, and Cucurbitaceae (Cucurbitoideae) (Federov, 1969; Jeffrey, 1980; Cronquist, 1981). The chromosomes of *Ceratiosicyos* are very small and in this respect agree with those of Cucurbitaceae (Whitaker, 1933).

Phytochemistry. All three genera of Achariaceae are strongly cyanogenic (sodium picrate paper test). This supports an affinity particularly to Passifloraceae and Flacourtiaceae. Cucurbitaceae are essentially noncyanogenic (Gibbs, 1974). Work is in progress to determine whether cyclopentenoid cyanogenic glycosides (apparently confined to Flacourtiaceae, Passifloraceae, Malesherbiaceae, Turneraceae, and perhaps also Caricaceae) are involved (Gershenzon & Mabry, 1983; Harborne & Turner, 1984; Spencer & Seigler, 1985). Chemical analysis of *Ceratiosicyos laevis* showed that it does indeed contain the cyclopentenoid cyanogenic glucoside, gynocardin (S. R. Jensen & B. J. Nielsen, pers. comm., 1986). Gynocardin has hitherto been found in Flacourtiaceae and Passifloraceae only (Harborne & Turner, 1984). Provisional tests on all three genera showed that iridoids are absent.

Fungal or animal parasites. Members of the butterfly family Acraeidae frequently breed on plants of the Passifloraceae and occasionally also on Flacourtiaceae and Turneraceae (Williams, 1969). In southern Africa, *Acraea horta* L. breeds almost exclusively on *Kiggelaria africana* L. (Flacourtiaceae). Species of *Passiflora* L. have also been recorded as food plants (e.g., Van Son,

1963); but despite the abundance of both butterfly and *Passiflora* spp. in Pretoria gardens, no larvae have yet been recorded on the latter species. However, plants of *Ceratiosicyos* and *Guthriea* introduced into the University of Pretoria botanical garden were immediately spotted by *Acraea horta,* which (as in the case of *Kiggelaria*) circle the vicinity of the plants for most of the day. Oviposition occurs on both species. The larvae survived and butterflies were reared. Nearby species of the Passifloraceae and Cucurbitaceae were ignored. Notes on the biochemical relationship between *Acraea* and *Kiggelaria* are provided by Raubenheimer (1987).

Conclusions and relationships. Achariaceae are a well-defined family with the three taxonomically isolated genera. The hypogynous flowers with sympetalous corollas and swollen trichomes on the anthers clearly knit the three genera together. The family is clearly related to Passifloraceae and Flacourtiaceae and, to a lesser degree (particularly in stamen morphology), to Cucurbitaceae. It is regarded as an ancient offshoot derived from the flacourtiaceous stock from which Passifloraceae and perhaps Cucurbitaceae were derived. Achariaceae may be an important link between the Cucurbitaceae and the hypogynous Violales.

MYROTHAMNACEAE
Niedenzu in Engler & Prantl

Description. Small, sympodially branching, ascending, dioecious shrubs to ca. 0.5 (>1) m tall, with glabrous branches, each with a terminal inflorescence. Lateral vegetative branches largely developed as short shoots. Leaves opposite-decussate, small, with broad, sheathing base, stipulate, epetiolate, cuneate, obtriangular-obovate, flabellate-plicate, with distal half rounded and dentate; venation palmate to parallel from the base, glabrous, firm, capable of strong desiccation, aromatic-scented, the epidermis having cells with balsam or essential oils. Stipules simple, lateral, toothlike. Inflorescences determinate or (usually the female) indeterminate, i.e., with or without a terminal flower, spikelike, with flowers (or floral triads) at least basally in the inflorescence opposite and in axils of foliose (the lowest) or bracteose leaves, unisexual, with either male or female flowers. Flowers sessile, bibracteolate (or without bracteoles), unisexual, actinomorphic or by loss of some "tepals" bisymmetric or zygomorphic, hypogynous or atepalous, with 0–4 scales here interpreted as "tepals" and with either 3–8 distinct or (with the filaments) basally connate stamens or a 3–4-carpellary pistil. Bracteoles small, those of the lowest flower in the inflorescence of *Myrothamnus moschata* Baill. normally with lateral, ebracteolate flowers; bracteoles of upper flowers without buds, sometimes missing. "Tepals" lanceolate, 1–4 (or more), or missing, bracteose, when 4 sometimes fused at the very base. Stamens (when 4 in terminal flowers with 4 "tepals" alternating with these): filaments cylindrical, distinct or basally connate, erect; anthers basifixed (of "undifferentiated type"), 2-thecate, 4-sporangiate, narrowly obovate, with a distinct connective tip; thecae dehiscing with a longitudinal lateral slit. Pollen grains dispersed as tetrads. Pistil of 3–4 carpels fused only centrally and in the ovary region, thus 3–4-lobate in transection, 3–4-locular; each locule continuing gradually in a separate, stout, erect or slightly recurved stylodium adaxially with a decurrent, introrse, marginally ± undulate stigmatic surface almost as long as the stylodial branch. Ovules numerous, on central-axile placentae, anatropous. Fruits dry, capsular, ventricidally dehiscent. Seeds numerous, small, ovoid, with rather thin, reticulate seed coat and with abundant, oily endosperm and a relatively small embryo (Cronquist, 1981).

General information. Myrothamnaceae consist of one genus *Myrothamnus* Welw. with two species: *M. moschata* Baill. in Madagascar, and *M. flabellfolia* Welw. in Namibia, Angola, Transvaal of South Africa, Zimbabwe, Zambia, Mozambique, Malawi, and Tanzania (see Weimarck, 1936). At least the latter species grows on exposed, horizontal granite or sandstone rocks at altitudes of ca. 900–1,200 m, in temporarily arid regions. It is well known for its extreme drought resistance of the leaves (Vieweg & Zeigler, 1969), which exceeds that of most or all other flowering plants. Dried leaf branches, with leaves having a water content of only 7–11%, are extremely resistant both to cold and hot temperatures. When placed in water for ca. 7 hours, such branches have taken up water and retained their normal functions and have thus proven to be alive.

Treatment in the literature. *Myrothamnus* has normally been placed in a separate family, Myrothamnaceae, often in Hamamelidales, but was included in Hamamelidaceae by, for example, Bentham & Hooker (1867) and Baillon (1872).

Tippo (1938) found anatomical support for a hamamelidalean affinity, and this was further emphasized in the works of Niedenzu & Engler (1930), Gundersen (1950), Hutchinson (1959, 1973), Takhtajan (1959, 1969, 1980), Schulze-Menz (1964), Cronquist (1968), Endress (1977), and Dahlgren (1975, 1980a, 1983). The Myrothamnaceae have also been placed in Rosales, e.g., by Wettstein (1935). Thorne (1976, 1983), on the other hand, considered Myrothamnaceae as members of his order Pittosporales suborder Bruniineae, relating them with Geissolomataceae, Bruniaceae, Grubbiaceae, Roridulaceae, and Hydrostachyaceae. Carlquist (1978a) basically supported this view but also found wood anatomical similarity with Hamamelidaceae and Cunoniaceae.

Pollen morphology of Myrothamnaceae is, however, different from that in the mentioned families and, according to Erdtman (1952), similar to that in *Hedycarya* J. R. & G. Forst. of Monimiaceae, a point also discussed by Jäger-Zürn (1966), who stressed similarities between *Myrothamnus* and *Cercidiphyllum* (see later text).

Macromorphology. The infraspecific variation of *Myrothamnus flabellifolia* was described by Weimarck (1936) and concerns mainly shape and size of leaves and length of inflorescences. The morphology is described in detail by Jäger-Zürn (1966) and Puff (1978).

The plants grow in shallow soil and the root system is largely horizontal, not penetrating the soil more than ca. 10 cm (Child, 1960); ramifications into rock crevices, however, may have been overlooked (Carlquist, 1976a)

Male inflorescences frequently have a terminal flower; and as the lowest flowers often have lateral flowers in the axils of their bracteoles, the inflorescence can be classified as a panicle (at least as panicle-derived). Similar determinate inflorescences occur in several genera of Hamamelidaceae (Endress, 1978) and in Buxaceae. The flowers, especially in *Myrothamnus moschata,* often have 1–4 further scalelike floral leaves ("Hochblätter" sensu Jäger-Zürn, 1966) besides the two transverse prophylls. The nature of these, in our opinion, can best be interpreted in either of two ways: 1) if the flower is terminal on the main shoot or on the lowest lateral branches of the inflorescence (these flowers are the ones that generally have four floral leaves), the floral leaves may be interpreted as further pairs of densely crowded prophylls; or 2) they can be interpreted as tepals (presumably homologous to sepals in Hamamelidaceae), which are in the state of being lost in this wind-pollinated group.

Anatomy. The wood anatomy (Tippo, 1938; Carlquist, 1976a) is characterized by the presence of long, narrow vessels with oblique perforation plates of reticulate-scalariform type, with numerous bars. Lateral pitting of the vessels is alternate. All imperforate vascular elements are tracheids with bordered pits. The rays are exclusively uniseriate and composed mostly of erect cells (and a few square cells), all without crystals. Axial parenchyma is absent, a feature in which the Myrothamnaceae differ from nearly all other families with which they are normally associated (Carlquist, 1982). Wood anatomy of the Myrothamnaceae resembles, that of, for example, Roridulaceae, Hamamelidaceae, Geissolomataceae, and Grubbiaceae (Carlquist, 1982).

Leaf anatomy studies have been encouraged by the great reputation that *Myrothamnus* has in terms of drought resistance (Marloth, 1925; Grundell, 1933; Zemke, 1939; Child, 1960; Hambler, 1966; Mauve, 1966; Puff, 1978). The nodes are unilacunar (with a "common gap"; Puff, 1978), and the leaf bases are decurrent, continuing as longitudinal ridges on the young stems. Abscission of the leaves occurs in a zone above the leaf base, just below the lamina (Grundell, 1933). The leaf sheath inside the adaxial epidermis has a tissue rich in crystal druses. The leaves, when dry, shrink and fold plicately. The stomata are present on both leaf surfaces and are restricted to the folds, thus concealed when the leaves are dried out. The stomata are anomocytic but the surrounding epidermal cells are somewhat smaller than the other cells of the epidermis. The venation of the leaf is largely palmate, with reticulate, anastomosing minor veins throughout. The epidermis of the upper leaf surface has larger cells than that of the lower. Some epidermal cells (on both surfaces, but more frequent on the upper) are enlarged, inflated, thin-walled, and filled with balsam (resins). Layers of cells rich in tannins are concentrated in the subepidermal 1–2 layers on the lower side of the leaves along the main veins. Ultratructurally, the chloroplasts of *M. flabellifolia* possess a unique type of granum (Wellburn & Wellburn, 1976).

Pollen morphology. The pollen grains in Myrothamnaceae are dispersed as primarily tet-

rahedral tetrads (Erdtman, 1952; Van Zinderen-Bakker, 1956). They are psilate and ± inaperturate, although Erdtman was inclined to regard the thin distal surfaces as "faintly delimited colpoids." Tetrad pollen is unusual in wind-pollinated taxa. Puff (1978) associated this condition with the multiovulate carpels (greater chances for fertilization of the numerous ovules). The pollen morphology is different from that in most other families generally associated with Myrothamnaceae (also see Zavada & Dilcher, 1986).

Embryology. A description of the embryology (both species) was given by Jäger-Zürn (1966), from which the data mentioned here are taken. The anther wall is 5–6-layered, consisting of epidermis, endothecium (1–2 layers), 1–2 layers of compressed cells, and the tapetum, which is secretory and consists of 2-nucleate cells. Microsporogenesis is simultaneous, and the mature pollen grains of the tetrads are 2-celled.

The ovules are numerous, anatropous, with dorsal raphe, crassinucellate, and bitegmic, with either the outer (*M. moschata*) or the inner integument (*M. flabellifolia*) being longest and forming the micropyle. The embryo sac development is of the *Allium* type (bisporic). The embryo sac is covered by 2–3 cell layers excluding the nucellar epidermis. Endosperm formation is nuclear. Presence of a hypostase is not mentioned, nor is a hypostase illustrated by Jäger-Zürn (1966).

Of these features, the tetrad pollen and the *Allium* type embryo sac stand out as particular to Myrothamnaceae. Other features largely agree with those in Hamamelidales but also with other orders and are of general occurrence.

Chromosome number. According to Puff (1978), the chromosome number in *M. flabellifolia* is $n = 10$.

Phytochemistry. Myrothamnaceae are characterized by the production of balsam in large, inflated epidermal cells; but the composition of the balsam does not seem to have been investigated (in spite of the fact that *Myrothamnus* is sometimes used for medical purposes; Hegnauer, 1963). Bate-Smith (1962) identified—in leaves—ellagic acid, quercetin, kaempferol, p-cumaric acid, sinapinic acid, and p-hydrobenzoic acid, as well as vanillinic and syringic acids and (derived from leucocyanidins) cyanidin; but not caffeic acid, myricetin, or leucodelphinidin. In evaluating these results in relation to the flavonoid contents in Hamamelidaceae and some related families, Jay (1968a) noted similarities between Hamamelidaceae and Myrothamnaceae; *Cercidiphyllum* Sieb. & Zucc. (Cercidiphyllaceae) agrees perhaps even better with Myrothamnaceae in flavonoid contents than do the Hamamelidaceae (also see Giannasi, 1986).

Crystal druses (probably calcium oxalate) are abundant in the leaves of *Myrothamnus.*

Conclusions and relationships. Endress (1977), in a morphological and evolutionary overview of the Hamamelidales, accepts Myrothamnaceae as good members of the order; while Jäger-Zürn (1966) expresses more reservation, giving particular attention to similarities between Myrothamnaceae and Cercidiphyllaceae.

Arguments for relationships between *Myrothamnus* and *Cercidiphyllum* are largely morphological, (e.g., opposite leaves (on long shoots), presence of stipules, similar leaf venation, unisexual floral clusters, similarity of stamens and carpels) but include some embryological features (except the type of endosperm formation), notably the poorly defined colpoid apertural areas of the pollen grains. Wood anatomy (scalariform perforation plates, heterocellular wood rays), and the flavonoid pattern are also similar in *Myrothamnus* and *Cercidiphyllum.* A parallel adaptation to wind dispersal may account for some of the morphological similarities. *Cercidiphyllum* differs conspicuously from *Myrothamnus,* however, with regard to the separate pollen grains, the *Polygonum*-type embryo sac, the cellular endosperm formation, the one-ovuled ovaries, the chromosome number ($n = 19$), and the carpels, which are separate with their stigmatic surfaces directed outward (instead of inward), indicating that the pistil groups represent pseudanthia rather than single flowers. *Cercidiphyllum,* like the Hamamelidaceae, lack balsam cells.

Arguments pro and contra close relationships between *Myrothamnus* and the Hamamelidaceae are about equally strong regarding Cercidiphyllaceae. Also the Hamamelidaceae have separate pollen grains, *Polygonum*-type embryo sacs, different chromosome numbers, and fewer ovules in the ovaries. The majority of the characters of various kinds are, however, similar in Myrothamnaceae and Hamamelidaceae.

Further, the Buxaceae, placed by Thorne (1983) in the same order as Myrothamnaceae (Pittosporales), show conspicuous morphological similarities with this family (in leaf, inflorescence,

floral details), similar wood anatomy (scalariform perforation plates, heterocellular wood rays), and agree in having unilacunar nodes and partly the same chromosome number ($n = 10, 14$). There are, however, differences in the stomata, stipules are lacking, ovules are fewer, ellagic acid is lacking, balsam cells are lacking, particular alkaloids are present. Thus the Buxaceae are clearly different from the Myrothamnaceae.

Geissolomataceae (mentioned earlier), which are insect pollinated and therefore lack the wind-pollination syndrome of character states found in all the above-mentioned groups, also show a number of similarities to Myrothamnaceae.

The collected evidence supports most strongly that Myrothamnaceae are hamamelidalean, being closely related especially to Hamamelidaceae, Platanaceae, and Cercidiphyllaceae. They are probably also rather closely related to Buxaceae and Geissolomataceae, which are more loosely connected with the hamamelidalean complex. *Myrothamnus* differs conspicuously from all families of Hamamelidales in several characteristics and should be placed in a separate family.

Geissolomataceae Endlicher

Description. An evergreen, ascending shrub. Branches to ca. 1 m long, with 4 longitudinal ridges and with relatively inconspicuous, transverse leaf scars. Young branches ± densely clothed with long hairs. Leaves decussate, simple, entire, elliptic-ovate, leathery, to >20 mm long, yellowish green, with thickened, slightly recurved margins. Stipules small, subulate, darkish, situated on the sides of the short, petiolelike leaf base. Flowers solitary, terminal, on lateral short shoots, subtended by 3 pairs of decussate, bracteate, oblong or narrowly elliptic leaves, these increasingly large and petaloid (pink) above; vestigial floral buds often present in axils of uppermost bracts. Flower with short, sharply 4-angled pedicel, bisexual, monochlamydous, hypogynous, with 4 decussate tepals basally connate for a short distance. Tepals large, ovate, pointed, rose-colored. Stamens 4 + 4, attached basally to the floral tube; filaments long, erect; anthers ovate, dorsifixed, 4-sporangiate, with short, apical connective, longitudinally dehiscent; pollen grains dispersed singly. Nectar disc lacking. Ovary 4-lobate in transection, with 4 carpels fused centrally, each locule with 2 pendulous anatropous ovules attached centrally in the upper middle part of the ovary; stylodia basally and centrally separate but distally connate and twisted, separate apically and covered with stigmatic papillae adaxially. Fruit a hard, 4-lobed, loculicidal capsule enclosed in the persistent perianth. Seeds one per locule, reniform, smooth, ca. 3.5 mm long, with a short, whitish funicle. Embryo long, with linear cotyledons and short obtuse radicle. Endosperm present. (Figure 3.)

General information. The family is monotypic, consisting of *Geissoloma* Lindley & Kunth, with the single species *G. marginatum* (L.) A. Juss. It is restricted to the Cape, occurring in the Langeberg Mountains of the Swellendam and Riversdale districts. The species grows in scrub ("fynbos") vegetation at altitudes of 600 to 1,200 m.

Treatment in the literature. *Geissoloma marginatum* was first described under *Penaea* and was for a long time assigned to Penaeaceae, although considered aberrant within this family by Ventenat (1804). Kunth (1830) was the first to treat the plant as a separate genus. Geissolomataceae and Penaeaceae have usually been placed together either in Myrtales or Thymelaeales. The view that *Geissoloma* is related to Penaeaceae can be explained by several shared features, in particular the coriaceous, decussate leaves with minute stipules (these in intravaginal rows in Penaeaceae), the 4-merous, monochlamydous and (at least basally) syntepalous perianth, and the 4-merous superior pistil. The diplostemonous condition in *Geissoloma* was recognized early as a conspicuous difference, and later a number of anatomical differences between the two families were recognized by van Tieghem (1893) and Supprian (1894) and have later been further stressed, for example, by Carlquist (1975).

Baillon (1877) was perhaps the first to treat *Geissoloma* in Celastraceae, and a position for Geissolomataceae in Celastrales was also later preferred both by Takhtajan (1969, 1980) and Cronquist (1968, 1981). The bases for its position in Celastrales are weak: according to Cronquist (1981) this order offers the "least uncomfortable" position. The pollen morphology, according to him, is much like that in Celastraceae and Hippocrateaceae. Other features (primitive vessels, simple perianth, lack of nectary disc, lack of aril, free stylodia) in combination make a position in Celastrales difficult to justify, although each of these features occurs exceptionally in Celastraceae (a dubiously homogeneous

FIGURE 3. *Geissoloma marginatum* (L.) A. Juss. (Geissolomataceae).—A. Part of branch.—B. Leaf.—C. Leaf base with stipules.—D. Leaf margin, transverse section.—E. Hair from young leaf.—F–H. Bracts of three successive pairs, subtending the flower of a lateral short shoot.—J. Flower.—K. Stamen.—L. Anthers in different views.—M. Pistil.—N. Ovary, longitudinal section.—O. Pistil, upper part of ovary and stylodial bases.—P. Stylodial apices.—Q. Mature embryo sac with starch grains (from Stephens, 1910).—R. Young capsule.—S. Seed. Material: A, B, "Cape," sine coll. (LD); C, R, S, *Phillips 305* (SAM); D–P, *Taylor 3870* (PRE). See also Dahlgren & Rao, 1969.

family). Cronquist considers *Geissoloma* primitive in Celastrales and a possible link to the ancestral Rosales.

Stephens (1910) confirmed, on embryological grounds, that *Geissoloma* should be excluded from Penaeaceae, as it has, for example, a *Polygonum*-type embryo sac formation; but she did not remove Geissolomataceae from Myrtales, where the family was also placed by Gilg (1894) and even by Phillips (1951). Weberling (1963) took a similar view, which he based on the presence of the small stipules. Hutchinson (1926) placed both Penaeaceae and Geissolomataceae in Thymelaeales.

Thorne (1976, 1983) prefers treating Geissolomataceae, together with Myrothamnaceae, Grubbiaceae, Bruniaceae, Roridulaceae, and Hydrophyllaceae, in the suborder Bruniinae of his Pittosporales, all these families sharing some wood anatomical characteristics and most sharing a geographic concentration in southern Africa. We believe that this suborder is divisible into several units, of which Geissolomataceae and Myrothamnaceae have much in common, e.g., in floral morphology and embryology.

Dahlgren & Rao (1969), studying the floral anatomy, pointed out some similarities to Oleaceae and Salvadoraceae but noted that Geissolomataceae represent a more primitive level than these families. Dahlgren (1980a) and Dahlgren et al. (1981) later placed Geissolomataceae in Hamamelidales, and later still Dahlgren (1983) placed it in a separate order near Hamamelidales (Rosiflorae).

Macromorphology. Only a few notes on the floral structure of Geissolomataceae will be given here. The outer four stamens alternate with the four tepals, and the carpels alternate with the inner four stamens; thus the carpels alternate with the four tepals. The position of the outer four stamens in *Geissoloma* therefore corresponds to that of the petals in, for example, *Hamamelis* of the Hamamelidaceae. In *Myrothamnus moschata* of Myrothamnaceae (Jäger-Zürn, 1966), however, the perianth members, where four are present, are opposite the carpels. It is, however, uncertain whether the position of the floral parts in relation to each other in this case can be used for phylogenetic speculations.

The stylodial branches, which are free from each other along most of their length, are a feature shared by Geissolomataceae, Hamamelidaceae, Myrothamnaceae, and some more supposedly related families. In the last-mentioned families, the stigmas are conspicuously decurrent, while in Geissolomataceae the stigmatic papillae are restricted to the apical part of the stylodia. This difference is probably connected with the type of pollination: insects in Geissolomataceae, but at least predominantly by wind in the other groups. Long, decurrent stigmas are also characteristic of the (wind-pollinated) Fagales, considered, for example by Endress (1977), to be closely related to Hamamelidales. In this complex of orders the decurrent stigma may not necessarily represent the primitive character state.

Anatomy. According to Carlquist (1975), the vessels in *Geissoloma* are long and have oblique scalariform perforation plates with 12–33 bars. Fagerlind & Dunbar (1973) noted that in the vessels membranes may persist in part of the slits, suggesting low conductivity in these vessels. The imperforate elements of the axial secondary xylem is made up of tracheids only (Carlquist, 1975). The lateral walls of the vessels have opposite or scalariform perforations in the intervascular contacts. Axial parenchyma is diffuse and scanty and occurs in strands of 4–5 very long cells. Both multiseriate and uniseriate rays are present, the former with procumbent cells in the central portions and with square to erect cells in the periphery, the latter with square to erect cells only. One or two rather large rhomboidal crystals, and sometimes also numerous small crystals, of calcium oxalate may be present in the ray cells (Carlquist, 1975). According to Carlquist the wood anatomy of *Geissoloma* resembles especially Grubbiaceae (*Grubbia tomentosa* (Thunb.) Harms) and Bruniaceae (*Nebelia fragarioides* (Willd.) Kuntze), but also taxa of Hamamelidaceae. Internal phloem is lacking. The stem cortex contains stone cells and the cork arises in the outer part of the primary cortex.

The cells of the leaf margins are high and palisadelike, which makes the margins thickened (Dahlgren & Rao, 1969), while other epidermal cells are comparatively low. Stomata are restricted to the lower side of the leaves and are anomocytic. The hairs are unicellular and bibrachiate with one long and one quite short arm. A conspicuous palisade layer is present under the upper epidermis. A fiber sheath is present below the midvein.

As regards the vasculature of the flower (Dahlgren & Rao, 1969) the carpellary dorsals are separate from the perianth traces, while the traces

of the inner stamens are joined with the median traces of the perianth at the base. The ventral carpellary traces continue above the ovary into the stylodia. These features differ conspicuously in Penaeaceae.

Pollen morphology. The pollen grains (Fig. 4) are isopolar, radially symmetrical, 3-colporate, ± spherical, and have a polar diameter of ca. 20 μm (some asymmetrical ± 6-pantocolpate grains were also encountered). The exine is baculate-tectate, perforate, without further exine sculpturing. Perforations vary in size and are elongate or (mostly) isodiametric. The ora are lalongate and the colpus membrane smooth. Similar pollen morphology occurs in some genera of Hamamelidaceae but is also found in various other groups, e.g., in Celastraceae (see Cronquist, 1981), but not in Myrothamnaceae nor in Penaeaceae.

Embryology. The anthers of *Geissoloma* lack the thick connective typical of Penaeaceae. The anthers are bithecate and 4-sporangiate (Dahlgren & Rao, 1969) and have a well-developed endothecial layer with annular wall thickenings. Tapetum is probably glandular (further studies are needed to establish this). The pollen grains are dispersed separately.

The ovular morphology was studied by Stephens (1910), from which the following information is taken. The ovules are anatropous, crassinucellate, and bitegmic, with dorsal raphe. The micropyle is formed by the outer integument. There is some (but not complete) evidence that the embryo sac formation is of the *Polygonum* type. The embryo sac is 8-nucleate and filled with starch grains, which begin to disappear before fertilization. The three antipodials soon decrease in size and lose staining properties. It is clear that no hypostase is formed (cf. Bruniaceae and Grubbiaceae). The nucellus is composed of a central strand of elongated cells surrounded by starch-filled parenchyma, the latter being digested by the elongating embryo sac. Endosperm formation is not described by Stephens. A copious endosperm is formed and is only partly resorbed by the developing embryo. No endosperm haustoria develop. In the ripe seed the long embryo is surrounded by a fleshy endosperm. The embryo is straight and slender, with long, well-developed cotyledons. The funicular part of the seed becomes whitish and swollen and forms a collarlike caruncle.

Chromosome number. Unknown.

Phytochemistry. Little is known about the chemistry of *Geissoloma.* Some epidermal and subepidermal cells are mucilaginous. There are crystals in the ray cells of the wood, and rather small druses in the leaf epidermis and mesophyll. Chenery & Sporne (1976) reported high contents of aluminum (also found in Daphniphyllaceae, Cunoniaceae, Celastraceae, Icacinaceae, several families of Myrtales, etc.).

Conclusions and relationships. The combination of features found in Geissolomataceae is somewhat difficult to evaluate. Many character states are of general occurrence, and some of them (such as those associated with wood, the diplostemony, the isomery throughout the flower, the free stylodia, and those associated with embryology and pollen morphology) express a low level of specialization. Therefore *Geissoloma* could be judged as a primitive starting point, or at least as an unspecialized member of orders (such as Myrtales or Celastrales) although it lacks all or practically all the diagnostic features of them. Support for a position in Celastrales, where Geissolomataceae have been placed by Cronquist (1968, 1981), Takhtajan (1969, 1980), and Dahlgren (1975), includes the presence of small, simple stipules, tetramerous flowers, similar pollen grains, a rather similar embryology, a tendency of an aril on the seeds, and aluminum accumulation.

Support for a close relationship between Geissolomataceae and some of the families of the Pittosporales sensu Thorne (1983) (i.e., Bruniaceae, Grubbiaceae, Myrothamnaceae, Roridulaceae, Hydrostachyaceae, Buxaceae, Didymelaceae, Daphniphyllaceae, Balanopaceae, Pittosporaceae, Byblidaceae, and Tremandraceae) is based mainly on wood anatomy. Great embryological and morphological differences make unlikely a close relationship between Geissolomataceae and most of the last-mentioned families. However, relationships with Myrothamnaceae, Buxaceae, and Daphniphyllaceae are plausible. In fact, these three families, like Geissolomataceae, seem to be more or less closely associated with the Hamamelidales, in which Endress (1977) includes Myrothamnaceae. Embryological similarities between most of these families include the anatropous ovule with a dorsal raphe, the bitegmic, crassinucellate condition, absence of hypostase, and relatively well-devel-

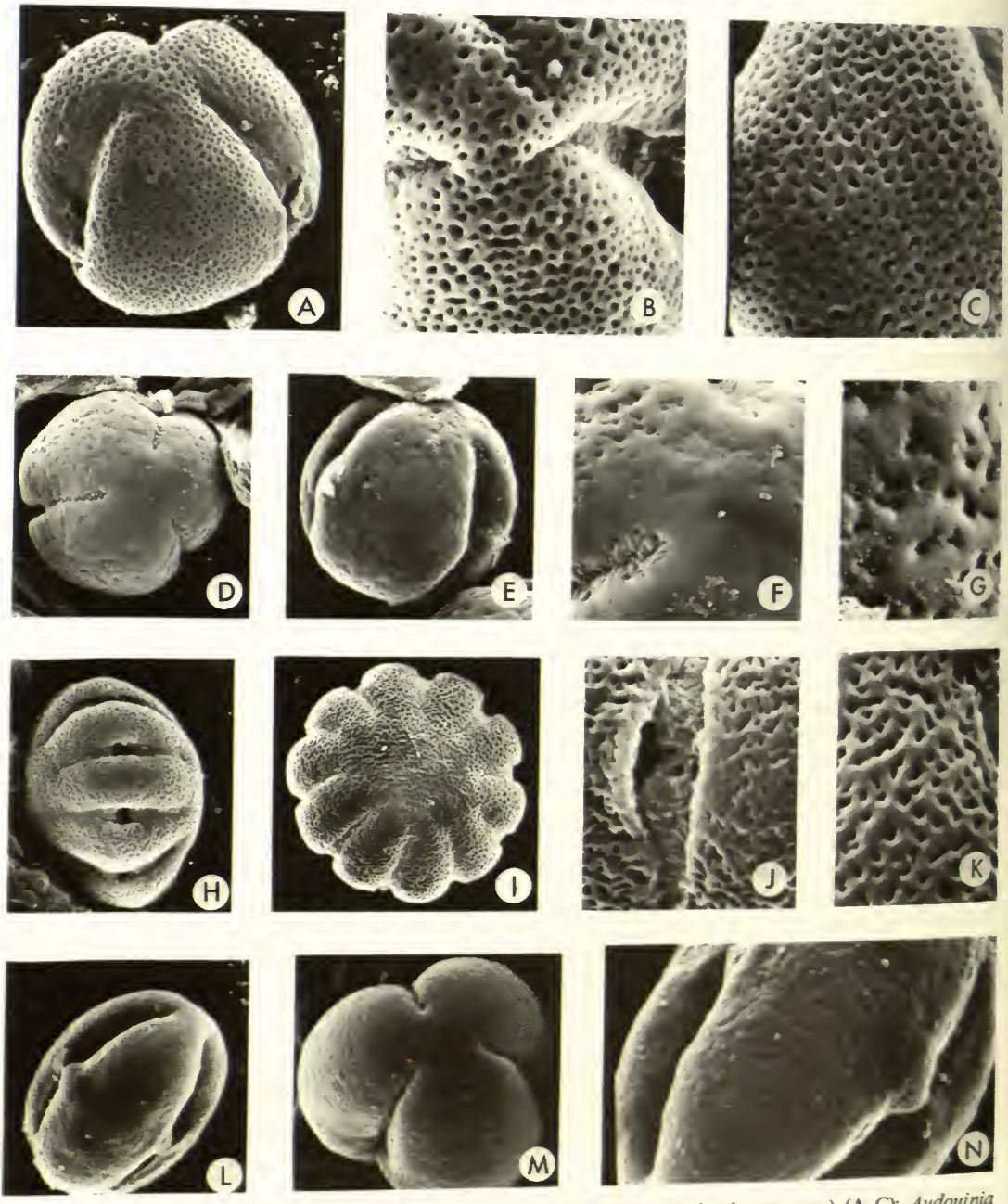


FIGURE 4. Pollen grains of *Geissoloma marginatum* (L.) A. Juss. (Geissolomataceae) (A–C); *Audouinia capitata* (L.) Brongn. (Bruniaceae) (D–G); *Lonchostoma monogynum* (Vahl) Pill. (Bruniaceae) (H–K); and *Grubbia rosmarinifolia* Berg. (Grubbiaceae) (L–N).—A, D, M. Pollen grains in polar or obliquely polar views.—E, H, L. In equatorial or obliquely equatorial views.—B, F. Details of apocolpal regions.—C, G, K, N. Details of mesocolpal regions.—J. Detail of aperture. Magnifications: A. ×2,500; B, C. ×5,000; D. ×625; E. ×650; F. ×1,500; G. ×3,750; H, I. ×800; J. ×3,750; K. ×5,000; L. ×2,000; M. ×2,850; N. ×4,750. Material: A–C. *Ecklon & Zeyher s.n.* (C); D–G. *Ecklon "58.8,"* (C); H–K. *Carlquist 4628* (C); L–N. *Goldblatt 4776* (C). (Preparation and photography by J. Praglowski.)

oped embryo albeit with endospermous seeds. These embryological similarities, however, represent common character states. With the similarities in wood (Carlquist, 1975) and floral features, the embryological concordance assumes more significance.

Perhaps most striking is the general similarity between Geissolomataceae and Hamamelidaceae sensu lato. Stipules, although larger than in Geissolomataceae and often caducous, occur in Hamamelidaceae. The coriaceous texture of the leaves in several families is the result of adaptive evolution as a response to a Mediterranean type climate. Evergreen, coriaceous, largely nondentate leaves also occur in some genera of Hamamelidaceae, e.g., in *Distylium,* where the inflorescences are terminated by a flower and bear lateral flowers or floral groups, the latter of which terminate with a (female or bisexual) flower (Endress, 1978), and where the pistil has free stylodial branches.

Also *Myrothamnus,* which Endress (1977) accepted as a member of Hamamelidales, has inflorescences terminated by a flower. This, as in Geissolomataceae and some Hamamelidaceae, is tetramerous. As described above under this genus, the terminal flowers of *M. moschata* have four phyllaries, which may either be interpreted as a perianth or as prophylls and which may even be basally fused (thus shown by Jäger-Zürn, 1966). In *Geissoloma* the four tepals do not differ conspicuously in texture, color, or shape from the bract pairs that enclose the flowers and could be interpreted as bracts, although they have always been regarded as true tepals).

With the available information, it is in our opinion justifiable to consider Geissolomataceae as rather closely related to the families in Hamamelidales and Buxales, less closely perhaps to Cunoniales, all in Rosiflorae sensu Dahlgren (1983). Whether or not Geissolomataceae can be sufficiently closely associated with any of these orders to be included in it is not clear. We chose, as in Dahlgren (1983), to treat the family in a separate order related to those just mentioned, in particular Hamamelidales.

Bruniaceae DC.

Description. Decumbent to erect shrublets, shrubs or small trees, from low to >4 m tall, with "ericoid" habit (Fig. 5A–C). Branches sometimes pubescent. Leaves alternate, densely set, often imbricate, simple, entire, generally small, pinoid, flat, subterete or trigonous, exstipulate or in some genera provided with small, simple, toothlike stipules; leaf apex in most genera (except *Audouinia* Brongn.) with brownish tips of dead, partly suberized cells. Inflorescences (or inflorescence clusters) terminal, spikelike, headlike, or rarely unifloral (*Thamnea* Soland.), the flower then terminal. Flowers sometimes, when aggregated in spikelike clusters (as in *Audouinia*), subtended by several imbricate bracts (Fig. 5E), each representing a unifloral short-shoot inflorescence, in headlike clusters subtended by the densely set upper leaves, these conspicuously enlarged and raylike in *Staavia* Thunb. Flowers small to medium-sized, bisexual, actinomorphic, 5-merous, tetracyclic, half-epigynous (rarely almost hypogynous) to completely epigynous. Sepals distinct almost to the base, short to rather long, well developed, often clothed on the outer side with unicellular hairs, generally (as foliar leaves) with brown tips. Petals corolline, glabrous, sessile or unguiculate (in *Audouinia, Linconia* L., and *Thamnea* Thunb.), and often provided with conspicuous (nectar-producing?) swellings on inner face (perhaps best developed in *Brunia* L.), distinct or (in *Lonchostoma* Wikstr.) fused into a variably long corolla tube (hence sympetalous). Stamens 5; filaments equally or unequally long, sometimes exserted beyond petals, inserted between petals, or, in *Lonchostoma,* very short or obsolete and inserted in the middle of the corolla tube; anthers dorsifixed, 2-thecate, 4-sporangiate, incurved in bud, introrse, sometimes sagittate with thecae basally apart, longitudinally dehiscent, rarely (*Linconia*) dehiscent only basally, upper parts of thecae being nonsporogenous. Pollen grains dispersed separately. Ovary wholly inferior or half-inferior, rarely almost superior, 2-locular, more rarely 1-locular (*Miniothamnea* Nieden.; *Berzelia* Brongn.), or (*Audouinia*; Fig. 5K) 3-locular; each locule with 1–4 (or even, in *Lonchostoma,* up to 12) apical or subapical, axile, pendulous anatropous ovules. Stylodia almost free to fused nearly to the top into a single style, often appearing as one style but with stylar branches standing close together, glabrous, erect; each stylodium or branch crowned by a capitate stigma; unilocular pistils with one stylodial branch only and probably unicarpellate. Fruit incompletely known (see Pillans, 1947), obviously generally dehiscent and a loculicidal capsule, but sometimes a nutlet or a schizocarp with 2 cocci (Marloth, 1925). Seeds arillate in some genera.

General information. Bruniaceae consist of 12 genera and ca. 75 species (Bond & Goldblatt, 1984) and are restricted to the Cape Province with the exception of one species, *Raspalia trigyna* Dümm., a ca. 1 m tall shrub endemic to the sandstone region of southern Natal and Pondoland. It is almost extinct, with at present only one plant known in the wild. The other taxa are largely concentrated in the winter rainfall regions of the southwestern Cape, where most grow on sand (mainly Table Mountain Sandstone (T.M.S.) products or marine sand) in fynbos vegetation. Some species are regionally common and form a conspicuous component of the scrub.

Treatment in the literature. Since the Bruniaceae were established, the family has generally been placed in widely circumscribed Rosales (e.g., in Hallier, 1912; Bessey, 1915; Wettstein, 1935; Schulze-Menz, 1964; Cronquist, 1981), but alternatively in Saxifragales (Takhtajan, 1969, 1980), Hamamelidales (Soó, 1953; Hutchinson, 1969), Araliales ("Umbelliflorae") (Lindley, 1853), or in its own order Bruniales (Nakai, 1943). Additionally, Thorne (1976, 1983) placed the family in Pittosporales suborder Bruniineae, and Dahlgren (1980a, 1983) in Cunoniales.

The picture thus seems rather confused. However, a common feature is that the family generally appears in a rosifloran connection, together with families around Saxifragaceae and Cunoniaceae, which are frequently rather closely associated, at least in German literature, with Hamamelidaceae. Also the Pittosporales are considered by Thorne (1983) to be allied to Hamamelidales, which Bruniaceae and other Bruniineae resemble in wood anatomical characters (Carlquist, 1978a). Lindley's (1853) treatment, with Araliales, is explained by the similar floral morphology (epigynous, 5-merous, 4-cyclic, 2-carpellary flowers; seeds with copious endosperm and small embryo, etc.). This order frequently has been closely associated earlier with Rosales sensu lato. In recent years, when Rosidae and Hamamelididae have been segregated as distinct subclasses by Takhtajan (1969) and Cronquist (1968), the need for a more precise establishment of the relationships has become necessary. In particular, possible relationships with the other members of Thorne's Pittosporales—Bruniineae (Grubbiaceae, Geissolomataceae, Myrothamnaceae, Roridulaceae, Hydrostachyaceae)—and with Hamamelidaceae, Cunoniaceae, and families of Saxifragales need to be considered. As a close relationship between Bruniaceae and Grubbiaceae has been stressed in particular on the basis of anatomical evidence (Carlquist, 1978a, 1978b; Thorne, 1976, 1983), the relationships between Bruniaceae and families of Ericales, where Grubbiaceae are frequently placed, must also be considered.

The Bruniaceae were revised by Pillans (1947), and the concepts and number of genera and number of species have changed little since then (see Bond & Goldblatt, 1984). Embryology was described for species of four genera by Saxton (1910), but observations were incomplete. Additional data provided by T. Brogaard Nielsen (unpubl. data) confirm and complement those of Saxton. Pollen morphological conditions were described by Erdtman (1952) and Van Zinderen-Bakker (1956), and notes are added here by J. Praglowski. Finally, Carlquist (1978a) carried out a detailed study of wood anatomy in the family, and Jay (1968b) studied the flavonoids in six genera. This material together forms the basis for the present conclusions.

Gross morphology. Stipules are present in *Linconia, Staavia, Tittmannia* Brongn., *Brunia,* and *Berzelia* but are absent in the other genera, including *Audouinia.* In other respects *Audouinia* stands out as probably ancestral, viz., in such character states as lack of brown leaf tips, terminal solitary flowers (on short shoots), 3-locular ovaries, only partial epigyny, unguiculate and free petals, equal stamens with filaments long and free from petals, nonsagittate anthers with parallel thecae, and nonarillate seeds. Further primitive features are manifested in pollen morphology and chromosome number (see later text). *Thamnea* and *Linconia,* with brown leaf tips and 2-locular ovaries, also have a number of presumably primitive features, *Thamnea* especially in the terminal flowers, each on a well-developed branch.

If this evaluation of character states is accepted, it would be more appropriate to consider a primitive genus like *Audouinia* than, for example, the more specialized *Lonchostoma, Berzelia,* or *Brunia* in an interfamilial comparison.

Further morphological studies are especially needed to make clear the inflorescence structure and the fruit types. In Pillans's revision (1947), the fruit was stated as unknown or imperfectly known in nearly all the genera.

The several aberrant features of *Lonchostoma* in Bruniaceae deserve special attention: the petals fused into a tube, the almost or completely sessile anthers inserted in the tube, the high ap-

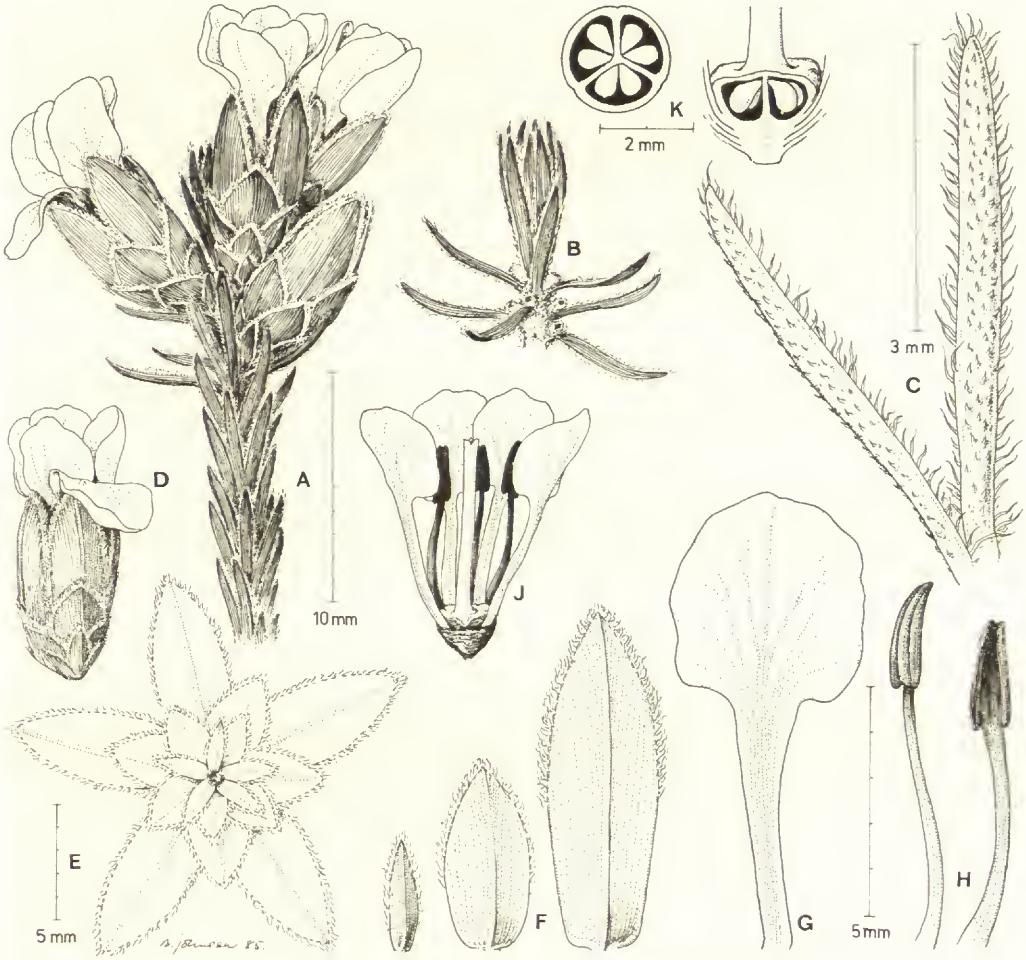


FIGURE 5. *Audouinia capitata* (L.) Brongn. (Bruniaceae).—A. Few-flowered inflorescence.—B. Shoot apex.—C. Leaves.—D. Flower with subtending bracteate leaves.—E. These bracts and calyx seen from the shoot base.—F. Bracts (left) and sepal (right).—G. Petal.—H. Stamens.—J. Flower; all sepals, one petal, and 2 stamens removed.—K. Ovary, transverse and longitudinal sections. (*Ecklon "58.8,"* (C).—Del. B. Johnsen.)

erture number, almost hypogynous flowers in some species, and the high ovule number (up to 12 per locule in *L. pentandrum* (Thunb.) Pillans). It is noteworthy that species of this genus have also been described under genera (*Gnidia* L., *Passerina* L.) of Thymelaeaceae. The anatomy (Carlquist, 1978a), chromosome number (Goldblatt, 1981), and other evidence, however, clearly support the position of *Lonchostoma* in Bruniaceae.

On the basis of floral similarities, Hall (1987) suggested a possible relationship between Bruniaceae and *Actinocalyx bohrii* Friss, a Cretaceous fossil angiosperm from southern Sweden (Friss, 1985).

Anatomy. The vessels in Bruniaceae are relatively long and have scalariform perforation plates with numerous bars, which are fully or vestigially bordered (Carlquist, 1978a). The perforations are generally ± aberrant in disposition of bars. Lateral wall pitting, intervascular and in vessel ray connections are scalariform to opposite. Axial parenchyma is largely diffuse. Rays are heterocellular with most or all cells upright, uniseriate and multiseriate in all species studied. Crystals, rhomboidal or smaller aggregates (druses), are present in ray cells. Amorphous dark-staining deposits (tannins?), sometimes in droplets, are also present in the wood (Carlquist, 1978a).

In all or most of these features the Bruniaceae agree with Grubbiaceae and Geissolomataceae (Carlquist, 1982), but the variation is greater in Bruniaceae and also approaches in nearly all characteristics those in Hamamelidaceae (see table in Carlquist, 1982). Also taxa of Cunoniales, Cornales, and some Ericales (not mentioned by Carlquist) are comparable in wood anatomy to Bruniaceae.

The leaves are flat or, more often, subterete and with centric structure. They are generally glabrous but have a very thick cuticle. Stomata are present all around the leaf except in *Linconia,* where they are restricted to the upper surface. They are principally anomocytic, although the surrounding epidermal cells are smaller than other epidermal cells. Hairs, when present, as on the margins of the leaves in *Audouinia,* are unicellular. A subepidermal palisade is developed all around the leaves, at least when these are narrow.

Pollen morphology. The pollen morphology in Bruniaceae has been briefly outlined by Erdtman (1952) and Van Zinderen-Bakker (1959). The data and microphotographs of *Audouinia* and *Lonchostoma* given here have been contributed by J. Praglowski. The pollen grains vary much in shape and aperture number, from prolate-spheroidal and 3–4-colporate, as in *Audouinia* (Fig. 4D–G) and *Linconia,* to oblate and 10-colporate, as in *Lonchostoma* (Fig. 4H–K). The exine is tectate with infratectal bacula. The tectal surface varies from almost psilate (*Audouinia, Linconia*) to rugulose and murate–reticulate (*Brunia*) bearing variably close and wide perforations, minute or none (*Audouinia*) to quite distinct (*Lonchostoma* and especially *Brunia*) (Van Zinderen-Bakker, 1959). The colpi have rounded (e.g., *Audouinia*) to pointed (e.g., *Lonchostoma*) ends and an almost smooth to distally granular colpus membrane. The ora are generally lalongate.

In pollen, as in other respects, *Audouinia* and *Linconia* stand out as supposedly ancestral in the family by having fewest (3) apertures and rounded colpal ends. The pollen surface in these two genera is unusually smooth in the family, resembling that in Grubbiaceae.

Embryology and seed. Saxton (1910), who studied four genera, found great agreement in the material. The ovules are unitegmic, with a massive, thick integument and a long micropylar canal. The nucellus is small and is generally described in subsequent literature as tenuinucellate. However, Saxton clearly states, and shows with an illustration, that the megaspore mother cell (and the early megaspore tetrad) is separated from the nucellar epidermis by at least one cell layer. Thus it is not strictly tenuinucellate, as in Ericales or Lamiales. Whether it should be termed "almost tenuinucellate" or "weakly crassinucellate" is a matter of definition. Embryo sac formation is of the *Polygonum* type. In the course of development, the cells above it are completely absorbed and by the second nuclear division have disappeared. It is often filled with starch grains in the 8-nucleate stage (as is also the case in, for example, Geissolomataceae and Retziaceae). The synergids are pyriform, the egg cell spherical, and the antipodal cells ephemeral. Saxton did not observe endosperm formation or the formation of endothelium, nor did he mention the ± strong development of the hypostase, although this is shown in one of the illustrations (*Brunia*).

Brogaard Nielsen's observations (on *Nebelia, Brunia,* and *Pseudobaeckea*) confirm Saxton's as regards ovular architecture. Starch grains are described as abundant in the embryo sac of *Nebelia.* Formation of an endothelium occurs and a hypostase is present and particularly prominent in *Brunia* and *Pseudobaeckea.* The mature seeds have a thick cuticle, copious endosperm, and a small embryo, and in all details agree well with Grubbiaceae. Dark-staining cells with amorphous material are abundant in the seed coat. The micropylar part of the endosperm in immature seeds stains dark, suggesting the possible presence of a micropylar haustorium, but this needs to be verified.

The embryological features of Bruniaceae are incompletely known, as are those in Grubbiaceae. However, the conditions so far available for the two families are similar and differ from those in Hamamelidaceae, Geissolomataceae, and Myrothamnaceae, in 1) the single massive integument, 2) the few-celled, though by definition dubiously "tenuinucellate" nucellus, 3) the well-developed hypostase, and 4) the presence of an endothelium.

In these features they approach the families of Ericales (sensu Dahlgren, 1983), although the nucellus is here more strictly tenuinucellate. The incomplete knowledge of endosperm formation (cellular in Ericales) and endosperm haustoria (generally present in Ericales) prevents any decisive conclusions for placing Bruniaceae (and/or Grubbiaceae) in this order.

Chromosome number. Audouinia, with $2n = 22$, is so far the only known member of Bruni-

aceae on the diploid level (Goldblatt, 1981). Other genera (*Staavia, Raspalia* Brongn., *Lonchostoma, Pseudobaeckea, Nebelia* Sweet) have n = 22 or n = ca. 22, or numbers centered around that number; *Brunia* has n = 20 or 23, and *Berzelia* n = 20 and n = ca. 21. Tetraploids and hexaploids occur, but are rare (Goldblatt, 1981). The basic chromosome number of Bruniaceae is probably n = 11; and *Audouinia* stands out in this, as in several other characters, as primitive in the family.

Phytochemistry. According to Jay (1968b), the flavonoids of Bruniaceae normally include leucoanthocyanidin, leucodelphinidin, generally also quercetin and traces of myricetin, but not ellagic acid or kaempferol. These last compounds occur in most Hamamelidales, Bruniaceae thus somewhat different from this order. Cunoniaceae also contain kaempferol. Methylated flavonols (isorhamnetin and methyl-3-quercetin) were detected in Bruniaceae (Jay, 1968b) and contribute to their distinctness. Iridoids were not detected in the samples studied by Jensen et al. (1975).

Conclusions and relationships. The available evidence points to a great agreement with Grubbiaceae in vegetative anatomy, embryology, seed morphology, and pollen, but not particularly with regard to more obvious characters, e.g., the alternate leaves (opposite in Grubbiaceae) and the pentamerous, petaliferous, haplostemonous flowers (tetramerous, apetalous, diplostemonous in Grubbiaceae). Yet studying the variation in Ericaceae, for example, such features are variable and should not be judged dogmatically. They have indeed been disregarded by Thorne (1976, 1983), for example, who admitted an even greater variation in floral construction within his Pittosporales suborder Bruniineae.

Future studies will show whether or not there is clear evidence to link Bruniaceae closer to Ericales. The anatomy is not particularly similar (although not extremely different either), while floral construction, embryological conditions, and pollen could well be compared to conditions of the least specialized Ericales (i.e., those lacking mycorrhiza and having longitudinally dehiscent anthers and pollen dispersed as monads).

Thorne (1976, 1983) associated Bruniaceae with Myrothamnaceae, a clearly hamamelidalean family as interpreted by Endress (1977), and with Geissolomataceae. These two families correspond closely with Hamamelidaceae in anatomy and embryology. These families as well as Cunoniaceae are, however, totally different from Bruniaceae (and Grubbiaceae) in embryological features. It seems desirable to maintain a clear distinction between Hamamelidales and allied groups (including Geissolomataceae) on one side and Bruniaceae and Grubbiaceae on the other.

Other relationships previously proposed (e.g., with Araliales) are not supported by anatomical and chemical evidence, for example, and can be dismissed.

As a provisional alternative it seems reasonable to treat Bruniaceae and Grubbiaceae in a separate order, Bruniales, near Ericales.

Grubbiaceae Endlicher

Description. Evergreen, richly and monopodially branched shrubs to ca. 2 m tall, basally with a single stem from a woody taproot or with several branches from a lignotuber (see Fig. 6). Young branches longitudinally ridged, tomentose. Leaves opposite-decussate, linear or very narrowly triangular-lanceolate, simple, entire, with nearly flat margins (*Grubbia tomentosa* (Thunb.) Harms), or ericoid, with conspicuously revolute, thickened margins, petiolate, glabrous to hirsute above, tomentose to minutely hirsute (especially in the grooves if present) below, dull or greyish green, exstipulate. Petiole short to distinct; leaf blade above petiole often (forms of *G. rosmarinifolia*) broadening abruptly and sometimes with distinct basal lobes. Leaf bases connected by a transverse, long-pubescent ridge or wing on each side across the stem. Inflorescences axillary, consisting of a floral triad with 2–3 flowers (*G. rosmarinifolia*) or a conelike determinate floral cluster of 6–20 flowers, the former enclosed by two transverse, bracteate, hyaline leaves, the latter by three small and one larger bract. Flowers small, bisexual, actinomorphic, tetramerous, monochlamydous (probably apetalous), diplostemonous, epigynous, and 2-carpellate. Tepals distinct, valvate, sepaloid, externally densely white hairy except on the margins, internally glabrous, shiny, pink to dark red. Stamens 8, four of these with filaments slightly longer than in the other stamens, opposite and basally attached to the tepals; filaments pale, linear, ending as a blunt tip beyond thecae; anthers dorsifixed, 2-thecate, 4-sporangiate but peripheral microsporangia nonfunctional, vestigial; dehiscence lateral-longitudinal along a C-shaped line, anther walls remaining as two valves attached centrally (Fig. 6J). Pollen grains dispersed singly. Ovary externally papillate-pubescent; stylar base surrounded by tissue (disc?) covered with erect pubescence.

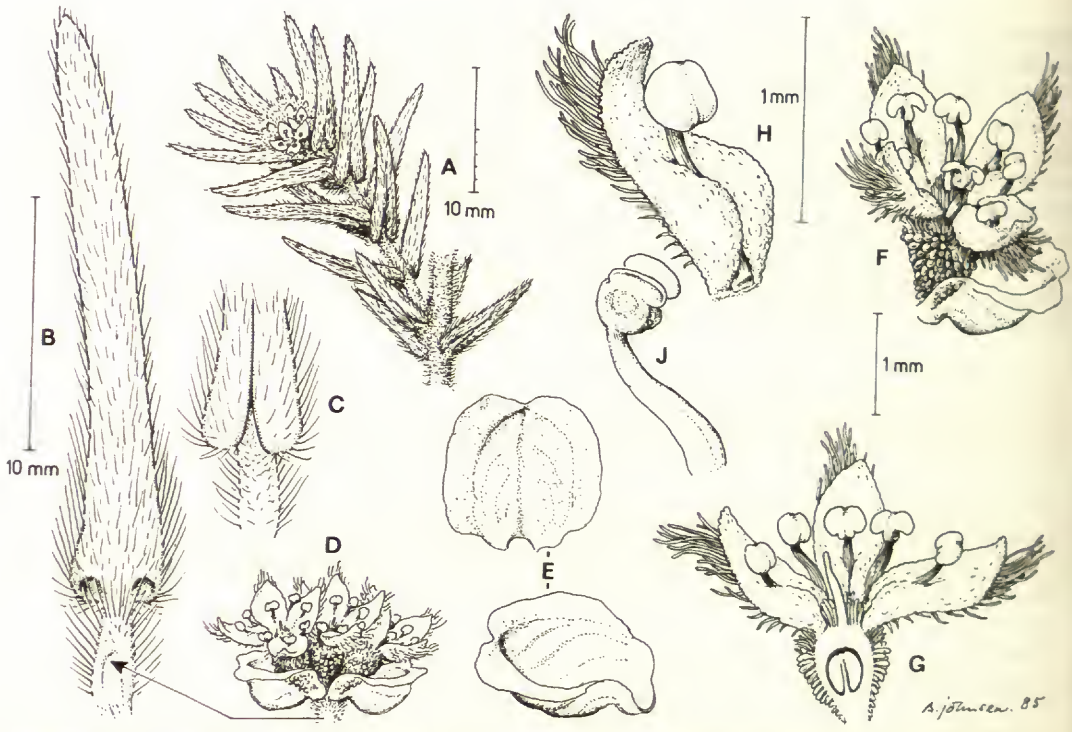


FIGURE 6. *Grubbia rosmarinifolia* Berg. (Grubbiaceae).—A. Floriferous branchlet.—B, C. Leaf, upper side to the left, with position of floral triad indicated.—D. Floral triad.—E. Bracts supporting the lateral flowers in the triad.—F. Lateral flower of triad and its bract.—G. Flower, longitudinally sectioned.—H. Stamen and tepal opposite this.—J. Stamen alternating with tepals, anther locules opened (note that one microsporangium in each theca is nonfunctional). (*Dahlgren & Strid s.n.* (LD).—Del. B. Johnsen.)

Style erect, straight, unbranched, smooth, with two short apical lobes, but appearing simple. Ovary initially 2-locular, becoming 1-locular by disintegration of upper part of septum above the insertion of the ovules, these solitary per carpel, pendulous from the upper part of the septum, anatropous. Fruits indehiscent, 1-seeded, drupaceous, often reddish, those of each inflorescence becoming laterally fused with each other into a coenocarpium. Seed with thin testa, endosperm copious, oily, embryo central, straight, the two cotyledons shorter than hypocotyl and radicle (for further information, see Carlquist, 1977a).

General information. Grubbiaceae consist of the single genus *Grubbia* Berg. with three species, *G. rosmarinifolia* Berg., *G. tomentosa,* and *G. rourkei* Carlquist (see Carlquist, 1977a). The genus is restricted to the Cape Province and ranges from the Cape Peninsula to the Uniondale District in the east and the Clanwilliam District in the northwest, growing in mountain fynbos mainly on sandy (T.M.S.) substrates.

Treatment in the literature. Grubbia was associated with Ericaceae early; when described by Bergius (1767) it was placed directly ahead of *Erica* L., while Jussieu (1789) associated it rather with *Empetrum* L. Later it is grouped with ericalean genera, e.g., by St. Hilaire (1805). This early association with Ericales is explained by the shrubby habit, ericoid leaves, and small, hairy flowers with two whorls of stamens. An ericalean affinity of Grubbiaceae was more recently supported by Fagerlind (1947) from a provisional embryological study of moistened herbarium material. Most of Fagerlind's observations are now supported by our own studies on FAA-fixed material collected in the field. A position in Ericales was also favored by Dahlgren (1975), Cronquist (1981), and Takhtajan (1980).

A close affinity between *Grubbia* or Grubbiaceae and the families of Santalales was expressed in the treatments of Bartling (1830), Bentham & Hooker (1862, 1867), Hutchinson (1926, 1959), Wettstein (1935), Harms (1935), Schulze-Motel (1964), and Cronquist (1968). This may originally have been based on an incorrect state-

ment in Hieronymus (1889) that the ovules (seeds) are "naked" (= ategmic). Van Tieghem (1897) made clear that the ovules are unitegmic, although this did not lead to an appropriate re-evaluation of the relationships of *Grubbia.* At present there is ample anatomical, morphological, and embryological evidence that Grubbiaceae are not related to the truly santalalean families.

Many authors from the time of van Tieghem (1897) have suggested Grubbiaceae to be closely related to Bruniaceae.

In recent years Grubbiaceae have been treated (Thorne, 1976, 1981, 1983) in an extended order Pittosporales (see under the previous three families), in suborder Bruniineae. It was considered by Carlquist (1977a) to be so similar to certain Bruniaceae in wood anatomical features that the families were not distinguishable. There are, however, considerable differences, especially in floral morphology (see the previous treatment of Bruniaceae). The similar geographic distribution stressed by Carlquist (1977a) and Thorne (1983) also supports a close relationship between the families of the Bruniinae.

Finally, Grubbiaceae have been included in Rosales sensu lato, to which Bruniaceae have often been referred. Affinities have been proposed between Grubbiaceae and Hamamelidales, based largely on wood anatomy and the tetramerous, bicarpellary flowers. Dahlgren (1980a, 1983) included both Bruniaceae and Grubbiaceae in Cunoniales.

In the present treatment, it has not been possible to resolve these differences.

Anatomy. A thorough account of the wood anatomy of Grubbiaceae was presented by Carlquist (1977a) and is the source of the data presented below. The vessels are long and have oblique perforation plates with many bars (16–43 in stem vessels). Lateral wall pitting is alternate on vessel-tracheid contacts, scalariform on vessel-ray contacts. The tracheids have bordered pits and are only slightly longer (or even shorter) than the vessels, which, as Carlquist stated, is a very rare condition. There are both multi- and uniseriate rays with upright or square cells, procumbent only in the center of multiseriate rays. The axial parenchyma is sparse and diffuse. As in Bruniaceae, a rhomboidal crystal or several small crystals occur in some of the ray cells. In these characters Grubbiaceae agree almost completely with some genera of Bruniaceae and with Geissolomataceae and differ only slightly from the Myrothamnaceae (axial parenchyma, crystals).

Pericyclic fibers in the young stems in all species form a discontinuous sheath (Carlquist, 1978a). The nodes, in contrast to nearly all Ericales, but as in Escalloniaceae and Grossulariaceae, are trilacunar. The leaf transection of *G. rourkei* and *G. rosmarinifolia* is "ericoid," i.e., margins, hairs, and stomata concentrate in two grooves formed between the midvein and margins on the lower side of the leaf. The epidermal cells of the upper leaf surface are large, and stomata are missing. All three species have a subepidermal layer of high palisade cells, among which are found groups of 2–4 cells, each with a crystal druse or a rhomboidal crystal. The stomata, all on the lower leaf surface, are anomocytic. All trichomes are unicellular and nonglandular. Foliar sclereids are lacking.

Bruniaceae also possess unicellular hairs, cells with crystal druses, and anomocytic (or cyclocytic) stomata, and lack foliar sclereids, but these features are common and give no decisive clue to a close relationship.

Pollen morphology. Pollen grains of *G. rosmarinifolia* (Fig. 4L–N) are isopolar, radially symmetrical, prolate (polar axis ca. 17 μm long, equatorial diameter ca. 12 μm), tectate-baculate, colporate, with narrow colpi and lalongate ora (J. Praglowski, pers. comm.). The tectum is psilate, not or inconspicuously pitted, tectal perforations being presumably lacking.

A rather similar basic, 3-colporate type with psilate-punctate tectal surface occurs in, for example, *Audouinia* Brongn., probably the least specialized genus of Bruniaceae.

Embryology and seed. Carlquist (1977a) described the ovules, one in each (incompletely delimited) locule, as pendent, anatropous, unitegmic, tenuinucellate, and provided with long micropyle. In the light of the otherwise embryologically similar Bruniaceae, the "tenuinucellate" condition needs to be verified by detailed study.

Young seeds of *Grubbia rosmarinifolia* (T. Brogaard Nielsen, pers. comm.) confirm previous statements that the ovules are unitegmic. The seed coat (Fig. 7) is ca. 5-layered and the epidermis has a thick cuticle. The endosperm forms a central core of rather distinct cell rows, 4–6 cells across; its micropylar as well as chalazal parts stain dark and appear to consist of dissolved cells, indicating that they represent ter-

minal endosperm haustoria. The fact that the endosperm forms distinct cell rows suggests (although this is yet not clear) that endosperm formation is cellular. The chalazal end has a conspicuous, ± globose hypostase.

On the basis of his provisional observations, Fagerlind (1947) came to the conclusion that Grubbiaceae are related to Ericaceae and argued that Grubbiaceae should be referred to Ericales. In embryological features, the similarity of *Grubbia* to Bruniaceae, which is not yet satisfactorily known either, is striking, even in such details as the well-developed hypostase.

Chromosome number. Unknown.

Phytochemistry. A test of *Grubbia rosmarinifolia* for iridoids proved negative (Jensen et al., 1975). There are no flavonoid reports for Grubbiaceae. Rhombic crystals and crystal druses occur in cells of the leaves, and crystals also occur in ray cells of the wood.

Conclusions and relationships. The Grubbiaceae, as pointed out by Carlquist (1977a), agree in several wood anatomical features with Bruniaceae. The two families are also conspicuously similar embryologically, e.g., in having a single, thick integument, a long micropylar canal, a weakly developed nucellus, a well-developed hypostase, a richly developed endosperm with cells in rows, and in having at one or both ends dark-staining areas indicating probable presence of terminal endosperm haustoria. It is, however, not clear whether the endosperm formation in either family is cellular. Additional similarities between Grubbiaceae and Bruniaceae include type of pubescence, occurrence and kinds of crystals, and the erect hairs around the stylar base. Grubbiaceae also resemble, to some extent, *Audouinia* Brongn., which seems to be primitive in Bruniaceae, in pollen morphology and in the lack of apical brown tips of the leaves and of stipules (loss of the latter probably derived). However, *Grubbia* differs from Bruniaceae in macromorphological features such as the opposite leaves and the floral construction. In the latter characters Grubbiaceae agree more with Geissolomataceae, which they also resemble in wood anatomy.

As discussed under Bruniaceae, both Grubbiaceae and Bruniaceae resemble Ericales in several features, although specializations typical of that order are lacking, notably tendency for having mycorrhiza, poricidal anthers, pollen tetrads, minute seeds, and ability to synthesize iridoid compounds. None of these features is consistent in Ericales, however, and a clear difference between the two families and this order is difficult to formulate, particularly if Bruniaceae and Grubbiaceae are confirmed in having similar cellular endosperm formation. Therefore we concur with Fagerlind (1947), Takhtajan (1980), and Cronquist (1981) in supporting a position in Ericales.

A position of Grubbiaceae (and Bruniaceae) in Cunoniales, as suggested by Dahlgren (1980a, 1983), for example, is consistent with floral structure and wood anatomy but is contradicted by several embryological characteristics. Regarding them as related to Myrothamnaceae and Geissolomataceae encounters similar difficulties, as these two families have bitegmic, pronouncedly crassinucellate ovules that lack a hypostase, and at least Myrothamnaceae have nuclear endosperm formation.

Finally, a santalalean affinity is contradicted especially by anatomical and embryological conditions.

Greyiaceae Hutchinson

Description. Deciduous and evergreen shrubs or small trees to 7 m; mature bole bark in treeforms thick, rough, and mainly longitudinally fissured; leafless older branchlets covered with a thin brownish layer of smooth-surfaced periderm, nodes and internodes indistinct; internodes green and photosynthetic, glabrous to densely pubescent, often with minute glandular hairs. Leaves crowded apically on the branchlets, alternate, petiolate; lamina simple, subrotund or ovate, up to 100(–130) mm long and wide, crenately or dentately lobed, coriaceous, either essentially glabrous or with a dense indumentum

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FIGURE 7. *Grubbia rosmarinifolia* Berg (Grubbiaceae). Young seed, longitudinal section, showing the thick unitegmic seed coat, the central endosperm with straight linear cell rows and with dark-staining regions at each end (suggesting terminal haustoria). Basally (bottom) is seen the well-developed hypostase. (Prepared by T. Brogaard Nielsen; FAA-fixed material supplied by I. Williams, from Voëlklip, Hermanus, Cape Province.)

of long, branched, multicellular but uniseriate hairs when young, often becoming glabrous with age, minute glandular hairs always present, producing a shiny layer of glutinous exudate often noticeably on particularly "glabrous" leaves and stem apices, palmately or subpalmatinerved; petiole distinctly expanded basally into a decurrent sheath congenitally fused with the preceding internode (sheath, petiole, and lamina are shed as a unit when the leaves fall); stipules wanting or very rarely with stipular outgrowths on the sheath lobes. Inflorescence a raceme with an aborted growing tip (panicle?), terminal, eventually displaced laterally by new leafy shoot(s) emerging below the peduncle. Flowers pedicellate, bracteolate, hermaphrodite, 5-merous, hypogynous, actinomorphic or slightly zygomorphic, campanulate or urceolate, distinctly protandrous, unscented, nectariferous. Sepals 5, free, imbricate, persistent. Petals 5, brilliant red or crimson, rarely white, free, imbricate, oblong, concave, much longer than the sepals, minutely ciliate, otherwise glabrous, partly reflexed or loosely coherent apically (*Greyia flanaganii* Bolus), fugacious with the remains sometimes retained by the persistent remains of the stamens. Disc extrastaminal, connected by five interstaminal ridges with the base of the ovary, fleshy, cupular with the margin crowned by ten staminodelike disc lobes; lobes with the distal portions subpeltate with a flattened suborbicular or narrowly ovate glandular area at the apex (*G. sutherlandii* Hook. et Harv. and *G. radlkoferi* Szyszyl.), or the lobes irregularly lacerate-dentate at the apex (*G. flanaganii*), more or less in pairs and curved toward the nearest epipetalous stamen, producing copious nectar, the dry remains persistent. Stamens 5 + 5, free, seemingly in a single series but most probably obdiplostemonous, episepalous stamens maturing first, exserted, red, persistent: anthers basifixed, 2-thecate, 4-sporangiate, erect in bud, latrorse, opening by longitudinal slits. Pollen grains shed as monads, whitish and clumping together when fresh. Ovary superior, sessile, deeply (4–)5(–6)-lobed, 5-locular; ovules ∞, arranged in two axial rows in each locule, axile placenta columnar or cylindric and developing from the invaginated margins of the (4–)5(–6) carpels; style simple, slender terete, subulate; stigma shortly 5-lobed, not papillate, wet; ovules anatropous. Fruit a subcylindrical chartaceous capsule, septicidal with folicular locules. Seeds numerous per locule, very small and elongated; testa membranous; embryo straight; endosperm fleshy, copious.

General information. A unigenic family of three species of soft-wooded shrubs or small trees endemic to southern Africa. *Greyia sutherlandii* and *G. radlkoferi* are shrubby deciduous trees from the slopes and rocky ridges of particularly the Drakenberg Mountains. The two species are closely related and tend to intergrade. *Greyia flanaganii* is a less robust shrub to 3 m high and occurs on rocky slopes in the eastern Cape, Ciskei, and Transkei. It is clearly distinct from the other two species in being evergreen and having a number of differences, particularly in floral morphology. A striking feature of the flowers is the bright scarlet petals that retain their color when dry. The species (particularly *G. sutherlandii*) are often cultivated as decorative ornamentals.

Treatment in the literature. In the past, *Greyia* was often placed in Melianthaceae, together with *Bersama* Fres. and *Melianthus* L. and associated with Sapindaceae (e.g., Hooker, 1873; Gürke, 1896; Scholz, 1964). *Greyia* was nevertheless usually placed in a unigeneric tribe, Greyieae, thus giving expression to the fact that its affinity with *Melianthus* and *Bersama* is not close. Gürke (1896) suggested that it would perhaps be more appropriate to place *Greyia* in a separate family. This step was taken by Hutchinson (1926), who recognized Greyiaceae and transferred it from Sapindales to Cunoniales, close to Escalloniaceae. This has subsequently gained wide acceptance in modern systems of classification, although there is still doubt as to the families with which Greyiaceae should be associated. Greyiaceae is placed among saxifragalean families by Takhtajan (1980), Cronquist (1981), Dahlgren (1983), and Thorne (1983). It is interesting that Harvey (1862) placed *Greyia* provisionally at the end of Saxifragaceae.

Macromorphology. Probably the most outstanding vegetative feature of Greyiaceae is the unusual way in which the leaves are positioned on the stems. The petiole is distinctly broadened at the base to form a sheath that is decurrent on the stem up to the preceding node. The sheaths are congenitally united with the stem, thus forming a kind of pseudocortex overlying the real cortex. Leaf trace bundles may pass from the vascular ring to enter the pseudocortex along the whole length of the internode. However, at least some of the major leaf trace bundles enter the pseudocortex at the level of the preceding node.

The sheathing nature of the leaves is further strengthened by the peculiar manner in which

the leaves abscise (first described by Schonland, 1914). At the end of the growing season the sheath, petiole, and lamina are detached together. Abscission of a leaf commences at the margins of the sheath near the base of the preceding internode. Loosening of the sheath is initiated by the formation of a periderm at the junction of the pseudocortex and the real cortex. The periderm clearly demarcates the outer boundary of the true stem. Leaf abscission proceeds acropetally along the leaf-bearing shoots. Schonland also noticed that, except in the case of the one or two uppermost leaves of a branch, the falling leaf usually carries away its axillary bud (also see Steyn et al., 1987).

Steyn (1974b), unaware of Schonland's (1914) work, also described leaf abscission in *G. sutherlandii* and *G. radlkoferi*. Steyn's paper is supplemented by a more detailed description of the associated anatomical features. She considered the so-called leaf sheaths in *Greyia* to be a broadened part of the cortex of the stem that contains the leaf traces. It would be interesting to speculate on the origin of these unusual leaf sheaths in *Greyia*, but this will not be attempted in the present account. Suffice it to say that we could not trace any reference to similar leaf sheaths in another group of plants.

Steyn's (1974b) conclusion that the leaves of *Greyia* have no sheaths is not accepted by the present authors. The free, upper margins of the leaf sheaths in *Greyia* are interpreted as sheath (vaginal) lobes ("Scheidenlappe"). Sheath lobes are common in Ranunculaceae, Berberidaceae, Saxifragaceae, Apiaceae, and occasionally also in Grossulariaceae (Weberling, 1975, 1976). Weberling noticed that stipulelike outgrowths may occur on the sheath lobes. Within some closely allied genera of the Saxifragaceae, stipules become gradually more distinct in the subsequent leaves of the same individual. Stipulelike outgrowths were recently noticed on the sheath lobes of a cultivated plant of *G. sutherlandii* (Fig. 8), possibly an atavism in this particular plant. The presence of these stipular appendages in *Greyia* suggests a saxifragalean affinity.

Whether the ovary in *Greyia* should be considered 5-locular or unilocular with five intrusive, but free, placentae has long been a matter of controversy (Schonland, 1914). Radlkofer (1890) indicated that the latter interpretation is erroneous and based on an artifact caused by the fact that the intrusive fused ventral margins of the carpels are often torn apart when the ovary is dissected. It is, however, clear from anatomical

FIGURE 8. Petiole base of *Greyia sutherlandii* (Greyiaceae). Note stipular outgrowths from the sheath lobes (only observed in one plant).

preparations (Steyn, 1977) that the intrusive central carpellary margins that form the placental column only fit tightly together around a central hollow. The borderline between the individual intrusive carpel margins remains clearly distinguishable, and this explains why the septa separate so readily during rough handling. Hutchinson (1959) considered the ovary of *Greyia* unilocular, but it is clear from the illustration provided that the intrusive margins of the carpels have separated during dissection. The illustration provided in Cronquist (1981) is closer to reality.

The carpels in *Greyia* are congenitally fused, and the ovary evidently develops from a cyclic apocarpous gynoecium, the likeness of which is still present in some members of the Rosiflorae (e.g., Crassulaceae). *Greyia* lacks the free styles common in syncarpous Cunoniales and Saxifragales, suggesting that the apparent weakly syncarpous nature of the ovary could be a secondary development towards apocarpy.

Flowers of *Greyia* are frequently visited by sunbirds, and the genus was regarded as orni-

thophilous by Vogel (1954). Honeybees probably also act as pollen vectors (Schonland, 1914).

Anatomy. Anatomy is of little help in establishing families related to *Greyia*. Heimsch (1942) considered anatomical differences sufficient to justify the segregation of Greyiaceae and Melianthaceae. However, he found no conclusive support from wood structure for the inclusion of Greyiaceae in Cunoniales. The heterogeneous rays seem to be common in Cunoniales, Saxifragales, and Rosales, but the storied fibers with simple pits (Metcalfe & Chalk, 1950) seem somewhat anomalous. The multilacunar nodes are relatively uncommon in the latter orders, although reported for example in some Cunoniaceae, Saxifragaceae, and Rosaceae (Cronquist, 1981). A uniseriate hypodermis in the lamina is a prominent feature of all *Greyia* species (Steyn, 1974a). A hypodermis is also present in members of the Cunoniaceae (Dickison, 1975), Rosaceae, and Saxifragaceae (Metcalfe & Chalk, 1979). Among the families possibly related, cortical vascular bundles have been recorded in Saxifragaceae s. str. (*Peltiphyllum* Engl.) (Metcalfe & Chalk, 1979).

An outstanding anatomical feature of Greyiaceae is the abundance of idioblasts containing raphide bundles. Raphides are almost unknown in those families sometimes considered related. Raphides occur in *Peltiphyllum* and *Rodgersia* A. Gray (Saxifragaceae s. str.) (Gibbs, 1974). Hydrangeaceae, in which the presence of raphides may be considered a family character, is quite different from Greyiaceae (e.g., unitegmic and tenuinucellate ovules) and best placed among the Corniflorae in the Cornales (Dahlgren, 1983). Similarly, Escalloniaceae (without raphides), thought by Hutchinson (1959) to be closely related to Greyiaceae, is placed with other families previously included in Saxifragaceae s.l. or Grossulariaceae s.l. in Cornales (Dahlgren, 1983).

Pollen morphology. According to Erdtman (1952), pollen grains are similar in *Greyia, Bersama,* and *Melianthus.* He does not consider that the pollen morphology supports transfer of *Greyia* to Cunoniales as a separate family. In a comprehensive survey of the exine stereostructure in Saxifragaceae s.l., Hideux & Ferguson (1976) concluded that *Greyia* is isolated but has some features found in genera such as *Montinia* Thunb., *Francoa* Cav., *Grevea* Baill., and *Davidsonia* F. Muell. The results of a numerical analysis confirm the fairly isolated position of *Greyia* and indicate some connection with *Tetilla* DC. and *Francoa* (Francoaceae). At least on pollen morphological grounds, *Greyiaceae* do not seem to be completely out of place among the families of Cunoniales and Saxifragales.

Embryology and seed. In *Greyia sutherlandii* the basal cell of the pro-embryo divides transversely (longitudinally in Melianthaceae), resulting in a T-shaped tetrad (Mauritzon, 1936). Embryogeny conforms to the Erodium variation of the Asterad type (Steyn, 1977; Steyn et al., 1986). According to Davis (1966), embryogeny in Saxifragaceae conforms to the Solanad type (Onagrad type recorded by Johansen (1950) in *Saxifraga* L.). In Rosaceae s.l., embryogeny is generally of the Asterad type, while Johansen (1950) recorded the Geum variation (similar to the Erodium variation). Embryogeny appears unrecorded in Cunoniales. On the basis of the very scanty data available, one can hesitantly say that embryogeny of Greyiaceae resembles Rosaceae more than Saxifragaceae—but this conclusion may be premature. Moreover, angiosperm embryogeny is not always considered significant in the classification and phylogeny of the angiosperms (e.g., Periasamy, 1977).

In *Greyia sutherlandii* the seed coat develops from both integuments. The outer epidermal layers of the integuments persist in the form of two fiber layers that serve as strengthening tissue in the mature seed coat. Other layers of the outer integument are flattened. The middle layer of the inner integument initially elongates radially, but eventually this layer as well as the inner epidermis is crushed (Steyn, 1977). Little is known about seed ontogeny in the orders Cunoniales and Saxifragales (Corner, 1976), thereby limiting any meaningful comparisons between seed coat structure in *Greyia* and members of these orders. Corner (1976) considered the seeds of Rosaceae and Hamamelidaceae typically mesotestal, which is unlike the structure in Greyiaceae. Saxifragalean families, however, seem to have small exotestal seeds (Kaplan, 1976; Krach, 1976, 1977), but it is always clear to what extent the inner integument may contribute towards the formation of additional mechanical layers. The full taxonomic significance of seed coat structure in *Greyia* remains undecided.

Chromosome number. Cytological evidence is consistent with a placement of Greyiaceae in Cunoniales and Saxifragales. The high base number of $x = 16$ or 17 ($2n = 32$–34) (Goldblatt, 1976) still awaits exact determination.

Phytochemistry. The flavonoid composition of *Greyia sutherlandii* does not support a connection with Saxifragaceae s.l., including Escalloniaceae, according to Jay (1967a, 1967b), who compared *Greyia* with 250 species representing 55 genera of Saxifragaceae s.l. In fact, he rather found support for a relationship of *Greyia* with Melianthaceae! Of particular interest was the discovery of kaempherol-3-methyl ether in *Greyia*—at that time only known from *Begonia* L. leaves (Jay, 1967b). However, kaempherol was not detected by Bate-Smith (1962) in *Greyia*—only ellagic acid and quercetin. Myricetin occurs widely in Saxifragales but has not been reported in Greyiaceae. On the other hand, the rarity of myricetin in Rosales clearly distinguishes it from neighboring orders (Gornall et al., 1979). In view of the suggested relation between *Greyiaceae* and the Rosales, the presence of β-ring-deoxy flavonoids in *Greyia* may be significant. These compounds are also present in Malaceae (= Rosaceae subfam. Maloideae) (Gornall et al., 1979), which, however, lack ellagitannins. The flavonoid profile for *Francoa* is unusual in Saxifragaceae and supports its placement in a separate family (Bohm et al., 1986). It lacks myricetin, thereby supporting a possible affinity between Francoaceae and Greyiaceae.

At certain times of the year *Greyia sutherlandii* emit a sweet scent (Killick, 1976b) in the field. This was detected even when the plants were not in flower. The source of the scent is still unknown. We have not recorded the same phenomenon in cultivated plants.

Fungal or animal parasites. In southern Africa, species of the fungus genus *Fusicladium* Bonorden were recorded as parasites almost exclusively on members of the Malaceae. There is one record of *F. effusum* Winter on *Carya illinoensis* (Wangenh.) K. Koch (Juglandaceae) (Doidge, 1950; Gorter, 1977, 1981, 1982). However, this fungus is no longer considered a *Fusarium* but a synonym of *Cladosporium caryigenum* (Ellis & Lang.) Gottwald (Gottwald, 1982). Malaceae are also favored in other parts of the world (*Review of Applied Mycology,* 1922–1961), although a few species of *Fusicladium* do occur in families apparently not closely related to Malaceae (one can always ask whether these are indeed members of the genus *Fusicladium*). In view of all the other evidence suggesting a relation with Rosales, it may be significant that *F. fuliginosum* Kalchbr. & Cooke is only known on *Greyia sutherlandii* (Doidge, 1950; Gorter, 1981). However, a possible Malaceae connection is dismissed by the presence of cyanogenic compounds in Malaceae (absent in Greyiaceae). Malaceae also differs from Greyiaceae in having exendospermous seeds.

Conclusions and relationships. Greyiaceae do not seem to be closely related to Melianthaceae. A few of the more conspicuous differences between the two families are listed in Table 1. Some have been elaborated in the text. The following more obvious features are shared by both families: flowers protandrous (Schonland, 1914; Steyn, 1977), extrastaminal disc (nectary), multilacunary nodes (Hilger, 1978b), stomata anomocytic, some species with glandular trichomes (Steyn, 1974a; Hilger, 1978a), pollen apparently similar (Erdtman, 1952), ovules anatropous, bitegmic and crassinucellate with a *Polygonum*-type embryo sac that develops from the chalazal macrospore, fertilization porogamous, endosperm nuclear in origin, epiphysis present in the embryos (all from Steyn, 1977), seeds albuminous with a small, straight, dicotyledonous embryo, tanniniferous and producing ellagic acid (Bate-Smith, 1962), traces of fructose oligosaccharides detected in both families (Pollard & Amuti, 1981). Most of these attributes are common in the Rutiflorae–Rosiflorae complexes.

The position of Greyiaceae in the Rosiflorae seems to be well founded. However, its closest family relationships remain unsettled. In gross morphological features of the flower and fruit, *Greyia* is strongly reminiscent of certain Saxifragales, Rosales, and particularly Cunoniales. Schonland (1914) considered the 10 stamenlike structures on the disc in *Greyia* to be outgrowths of the disc (lobes). However, these structures are so curiously suggestive of stamens (they are vascularized) that the disc in *Greyia* is here considered to be of staminodial origin (also see Steyn et al., 1987). It has probably evolved from an ancestor with a polystemonous androecium—not unlike some recent members of the Rosaceae and the genus *Eucryphia* Cav. (Eucryphiaceae). *Francoa* and *Tetilla* from Chile (often treated as Francoaceae) also have more than two whorls in the androecium, some which constitute staminodes. Flowers of *Greyia* have been described as obdiplostemonous (Schonland, 1914), although the stamens are seemingly placed in a single series. Androecia with an obdiplostemonous appearance were recorded in members of the Saxifra-

TABLE 1. Selected differences between Greyiaceae and Melianthaceae.

Feature	Greyiaceae	Melianthaceae
Leaf shape	simple, lobulate and toothed	pinnately compound
Stipules	absent (rudimentary stipules? rarely present—see text)	present, conspicuous
Petiole	sheathing at the base and congenitally fused with the preceding internode	not conspicuously sheathing at the base
Leaf abscission	leaves shed together with a strip of internode tissue	leaves shed in the usual manner
Inflorescence	perhaps basically a panicle (racemes with terminal flower absent but growing tip aborted) with all the flowers ± at the same stage of development; flowers may open ± simultaneously, or from the base, top, or middle of the axis; growing tip already inactive long before anthesis	racemes with flowers maturing and opening in an acropetal direction while young buds are apically added (monopodial) by the active growing tip
Flower symmetry	± actinomorphic	strongly (*Melianthus*) or vaguely (*Bersama*) zygomorphic
Nectary (disc)	annular	unilateral, rarely annular (some *Bersama* spp.)
Staminodes	present (disc lobes of some authors)	absent (although antherodes sometimes present in *Bersama*)
Stamens	5 + 5, free	4–5, sometimes basally connate
Ovule number	∞ in each locule	2–5 (*Melianthus*) or 1 (*Bersama*) in each locule
Ovule development	anatropous position of ovules develops through curvature of the funicular region	anatropous position of ovules develops through bending of the nucellus
Outer integument	triseriate	multiseriate
Hypostase	absent	weakly developed
Macrospore tetrads	either linear or T-shaped	linear
Secondary embryo sac nucleus	not hypertrophic	hypertrophic
Embryogeny	*Erodium* variation of the Asterad type (tetracellular proembryo T-shaped; suspensor present)	*Penaea* variation of the Asterad type (tetracellular proembryo globular; suspensor wanting)
Testa	develops from both integuments	develops from the outer integument
Seeds	minute, long, and narrow	relatively large, ± globose
Calcium oxalate	raphide bundles present	raphides absent but styloids present
Medullary vascular bundles (axis)	absent	often present
Hypodermis (leaves)	present	absent
Rays	heterogeneous	homogeneous
Wood fibers	storied	not (?) storied
Tylosis	often present in vessels	not reported
Septate fibers	absent	occasionally present (*Bersama*)
Intervascular pitting	scalariform and transitional	small, circular bordered pit pairs arranged alternately (mainly based on *Bersama*)
B-ring deoxyflavonoids	present	not reported
Bufadienolides	wanting	present

gaceae s.l. (Gelius, 1967). Floral morphogenesis in *Greyia flanaganii* has recently been discussed by Steyn et al. (1987).

Airy Shaw (1973) suggested a possible affinity between *Greyia* and *Ribes* L. (Grossulariaceae s. str.). Indeed, the leaf shape of *Ribes* is similar to that of *Greyia*. However, the similarities between the two taxa are clearly superficial. Although glandular trichomes and vascular bundle extensions are present in both groups, other important anatomical features do not support a close affinity (Bates, 1933; Steyn, 1974a). Moreover, the epigynous flowers, fleshy fruits, and pollen grains of *Ribes* are very different from those of *Greyia*.

Evidence from many sources indicates, beyond reasonable doubt, that Greyiaceae possess affinities with families included in Cunoniales, Saxifragales, and perhaps Rosales. Its position is obviously isolated (even suggesting placement in its own order), although there seems to be some connection with Francoaceae and Saxifragaceae s. str. (thereby supporting a provisional placement in Saxifragales). These three orders are closely related and probably arose from the same ancestral complex.

The confinement of Greyiaceae mainly to the eastern Transvaal escarpment and the Drakensberg suggests the family may be of temperate origin. Most families of the Cunoniales, Rosales, and Saxifragales have their maximum development in temperate regions. It may be significant that a number of relic southern hemisphere taxa are found among these orders (particularly Cunoniales). These taxa (e.g., members of Cunoniaceae, Davidsoniaceae, Eucryphiaceae, Francoaceae, Grubbiaceae, and Neuradaceae) have either a very restricted or a widely discontinuous distribution.

Heteropyxidaceae Engler & Gilg

Description. Deciduous and aromatic shrubs or small trees, many parts with abundant subepidermal secretory cavities; bark usually flaky; young branchlets puberulous. Leaves simple, alternate, petiolate, with rudimentary stipules; lamina linear-lanceolate, lanceolate or obovate-oblong, usually tapering at both ends, entire, abundantly dotted with minute subepidermal secretory cavities, glabrous, puberulous or pubescent; venation essentially brochidodromous, sometimes with a tendency towards acrodromous, one or two pair(s) of principal lateral veins often more prominent and with conspicuous hair-tuft domatia in the axils. Inflorescence a many-flowered panicle, terminal. Flowers small, usually dioecious by abortion, rudiments of the opposite sex always present and therefore appearing structurally hermaphroditic, actinomorphic, perigynous with the hypanthium cyathiform, creamish, scented, nectariferous. Sepals (4–)5, imbricate, persistent. Petals (4–)5, free, imbricate, inserted on the inner rim of the hypanthium and alternating with the calyx lobes, conspicuously gland dotted, fugacious. Disc well developed and lining the lower part of the hypanthium, orange-brown. Male flowers with stamens (4)5–8(10), free, exserted, essentially obdiplostemonous, erect in bud; anthers dorsifixed, 2-thecate, 4-sporangiate, latrorse, rarely introrse, longitudinally dehiscent, connective with 1–3 secretory cavities; pistillode turbinate with aborted ovules, style short and sunken, stigma indistinct. Pollen grains shed as monads. Female flowers with (4)5–8(10) staminodes, smaller than the stamens in male flowers and with antherodes; ovary superior, globose, 2(3)-locular; style inserted in a depression of the ovary apex, persistent and remaining green and fleshy for several months while the fruit develops, stigma capitate; ovules numerous on an axile placenta, hemianatropous, hypotropous, with a very short funicle. Fruit a small loculicidal 2(3)-valved capsule, partly included in the persistent calyx, globose. Seed numerous, minute, cresent shaped and variously compressed, slightly winged, brownish; without endosperm; testa smooth to reticulate, thin and papery; embryo more or less straight with two equal cotyledons.

General information. The single genus *Heteropyxis* Harv., with three species, is confined mainly to the eastern parts of southern Africa. *Heteropyxis natalensis* Harv. and *H. dehniae* Suesseng. are closely related and could be combined in a single species. *Heteropyxis canescens* Oliv. has a restricted distribution in the southeastern Transvaal and Swaziland and is clearly distinct from the other two species, although still closely related. A disjunct occurrence of *H. dehniae* in Angola has been reported (Martins, 1976).

The species of *Heteropyxis* are small to medium-sized trees occurring mainly in savanna but occasionally also in forest areas. Bruised twigs and leaves of all the species have a strong pleas-

ant, aromatic smell reminiscent of lavender, hence the common names "wild lavender" and "lavender trees."

Treatment in the literature. Summaries of the systematic treatment of *Heteropyxis* are supplied by Stern & Brizicky (1958) and Schmid (1980). *Heteropyxis* has been variously included in the Lythraceae, Myrtaceae, Rutaceae, and the unigeneric Heteropyxidaceae. It has also been compared with Rhamnaceae (although not actually included in it), and Hutchinson (1973) placed Heteropyxidaceae next to Eleagnaceae in Rhamnales. Schmid (1980) concluded that *Heteropyxis* is well placed in Myrtaceae and suggested its treatment as a subtribe Heteropyxidinae in the tribe Leptospermeae of the subfamily Leptospermoideae. Johnson & Briggs (1984) maintain Heteropyxidaceae as a separate unigeneric family related to Myrtaceae and Psiloxylaceae. Dahlgren in Dahlgren & Thorne (1984) doubtfully acknowledged Heteropyxidaceae as a distinct family, but Thorne preferred to include it in Myrtaceae as a subfamily Heteropyxidoideae.

Macromorphology. Stern & Brizicky (1958) referred to *Heteropyxis natalensis* and *H. canescens* as ". . . small evergreen trees or shrubs . . . ." Dyer (1975) likewise described *Heteropyxis* as evergreen. However, the species of *Heteropyxis* are deciduous (rarely semideciduous). In autumn the reddish leaves of *H. natalensis* make a colorful display. This seems to be completely at odds with Myrtaceae, which in all the references consulted is given as evergreen (always?). Deciduous woody species are, however, well known in Lythraceae and Punicaceae, for example.

A conspicuous feature of the leaves of *Heteropyxis* is the occasional presence of pocket domatia nearly always confined to a pair (rarely up to four pairs in *H. canescens*) of primary vein axils in the lower third or near the middle of the lamina. The subopposite pair(s) of lateral veins associated with the domatia are much more strongly developed than the other lateral veins. They are strongly curved apically, often to continue as a marginal vein. The presence of domatia is unusual in Myrtaceae, although it does occur in at least *Legrandia concinna* (R. A. Philippi) Kausel and several species of *Campomanesia* Ruiz & Pavon. (both Myrtoideae). The general venation pattern in *Heteropyxis* also appears to be atypical for Myrtaceae. The marginal vein of the lower part of the leaf lamina is, for example, often not continuous with the marginal vein formed by the loops of the (lower) pair of prominent lateral veins with domatia in their axils. In *H. canescens* some of the strongly developed secondary veins may run separately toward the leaf apex without the formation of a prominent and continuous marginal vein. The intercostal venation is also not very distinctly admedially orientated, a state considered basic to Myrtales (Schmid, 1980).

Subepidermal secretory cavities containing a yellowish oil are abundantly present in the leaves, young stems, flowers (including the petals), and fruits of *Heteropyxis*. The presence of these cavities in *Heteropyxis* has frequently been advanced as evidence in favor of a placement in Myrtaceae rather than Lythraceae. However, the taxonomic significance of the secretory cavities should not be overestimated. These structures have evidently arisen independently in taxa of various unrelated families. Secretory cavities are present throughout Myrtaceae but are rare in Lythraceae, reported in *Cuphea anagalloidea* St. Hil. (Solereder, 1908), although absent in the closely related *C. pascuorum* Mart. The leaves of a number of species of *Lagerstroemia* L. are described as punctate (Furtado & Srisuko, 1969), and it has now been confirmed that in at least *L. ovalifolia* Teysm. & Binn. these punctae are the result of abundant subepidermal secretory cavities (S. A. Graham, pers. comm.; Graham et al., 1986). These examples clearly underline the fact that the presence of secretory cavities could by no means always be interpreted as strong evidence for determining phylogeny. The presence of secretory cavities in *Heteropyxis* should therefore not be advanced as decisive evidence against an affinity with, or even inclusion in, Lythraceae. It is nevertheless true that Myrtaceae are outstanding in Myrtales for their secretory cavities and abundant production of essential oils (Dahlgren & Thorne, 1984).

Rudimentary stipules are present in *Heteropyxis* (Weberling, 1963) as they also occur in many other Myrtales, including Lythraceae and Myrtaceae (Weberling, 1984).

Plants of *Heteropyxis* are functionally dioecious or rarely monoecious (Fernandes, 1971). Flowers appear bisexual, but male flowers bear pistillodes and female flowers antherodes. Unisexual flowers are rare in Lythraceae and Myrtaceae (Schmid, 1980). The number of stamens in *Heteropyxis* varies from (4–)5–8(–10). Flowers with low stamen numbers (4 or 5) are obhaplo-

stemonous. Additional stamens are inserted opposite the sepals. Schmid (1980) considers *Heteropyxis* essentially obdiplostemonous, whereas Myrtaceae are usually polystemonous. Obdiplostemony is apparently absent in Lythraceae and has only rarely been reported in Myrtaceae. Schmid (1980), who places *Heteropyxis* in Leptospermoideae, admits that it is somewhat anomalous here in being the only known obdiplostemonous genus in this tribe.

Flowers of *Heteropyxis* are faintly scented and nectariferous. Honeybees appear to be the major pollen vectors. However, numerous other insect species (especially Lycidae, Coleoptera) visit the flowers as well. Considering their small size (2–3 mm diam.), the capsules are unusual in that they remain green and attached to the tree for up to 20 weeks before dehiscing.

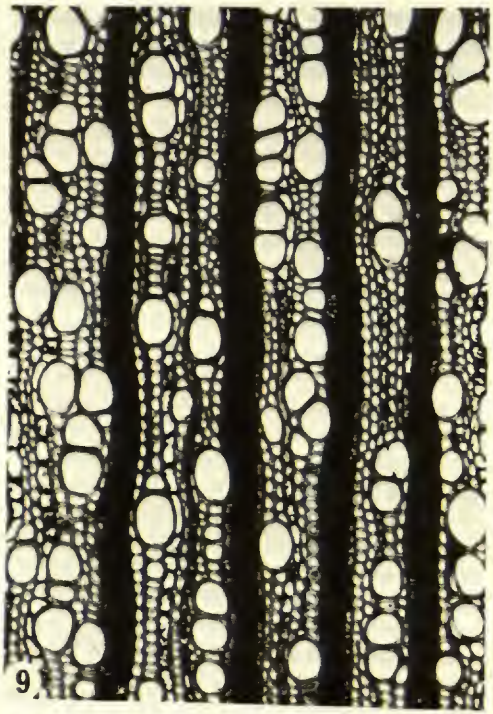
Anatomy. Stern & Brizicky (1958) studied various anatomical features of *Heteropyxis natalensis* and *H. canescens* and suggested the inclusion of *Heteropyxis* in Myrtaceae. However, they noted that their two wood samples (*both H. natalensis*) lacked the axial parenchyma characteristic for Myrtaceae. Other wood features claimed for *Heteropyxis* include pores solitary or in radial multiples, presence of fiber tracheids (no true fibers reported), gelatinous fiber tracheids in one sample (tension wood suspected), starch occurring as globular granules in ray cells and fiber tracheids, rhomboidal crystals in ray parenchyma cells only (in one sample), fibrous elements with amorphous deposits that may take the form of septa (no true septa present) and disjunctive ray cells.

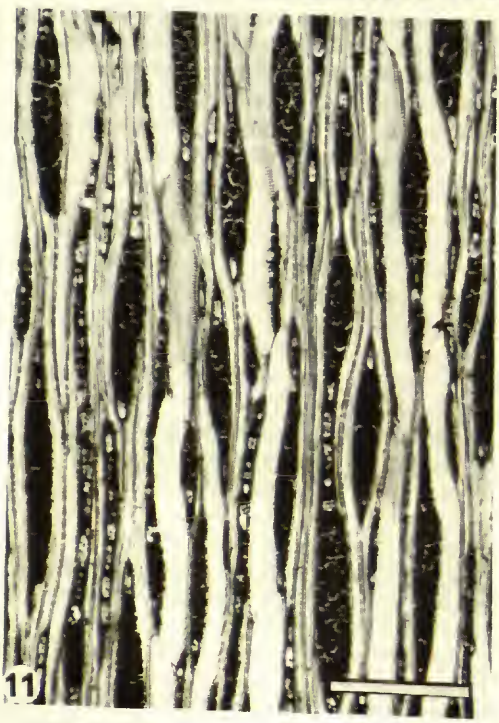
Baas & Zweypfenning (1979) compared the wood anatomical description of Stern & Brizicky (1958) with their own findings on the wood anatomy of Lythraceae and concluded that the general wood structure of *Heteropyxis* recalls Lythraceae rather than Myrtaceae. They nevertheless noted that the distinctly bordered pits of the fibers (fiber tracheids) and crystals in the ray cells of *Heteropyxis* differ from Lythraceae.

We have studied the anatomy of three mature wood samples of *H. natalensis* (vouchers: *Robbertse 1150* and *Van Wyk 6930, 6931* in PRU). A comparison of the results with the description of Stern & Brizicky (1958) confirmed some previous observations but also revealed major discrepancies (Figs. 9–11). Fibers of all three samples contain simple to minutely bordered pits and are considered typical libriform fibers and not fiber tracheids. These fibers are often septate, and previous claims that true septate fibres are wanting in *Heteropyxis* are rejected. The septa are darkly colored, but we cannot support Stern & Brizicky's interpretation that they are simply septalike amorphous deposits and not true septa. Gelatinous fibers were abundantly present in one but sparse in the other two samples (samples were taken from upright stems to avoid dealing with tension wood). Pores in radial multiples were common in all samples (>50% in one sample). Globular starch grains were noted mainly in the ray parenchyma cells and occasionally in fibers, particularly some which abut vascular rays. No crystals were present. All three wood samples lack axial parenchyma, thereby confirming previous observations. Disjunctive upright cells were present in the rays of all samples. The occurrence of crystals in wood can be extremely variable. However, the reported presence of crystals in the ray cells of *Heteropyxis* does not seem to be a characteristic feature and it probably does not merit much systematic attention.

If the emended wood anatomical description is compared with other Myrtalean families (e.g., Van Vliet & Baas, 1984) there can be no doubt that the wood anatomy of *Heteropyxis* closely resembles that of *Psiloxylon* Thou. ex Tul. and Lythraceae (also P. Baas, pers. comm.). A minor discrepancy seems to be the fairly wide heterogeneous rays (2–6-seriate), compared to the usual 2–3-seriate rays of Lythraceae (Baas & Zweypfenning, 1979; Van Vliet & Baas, 1984). However, rays up to four cells wide do occur in a number of Lythraceae (P. Baas, pers. comm.). Within the Lythraceae, the genus *Tetrataxis* Hook. f. from Mauritius seems to provide the closest match in wood anatomy. *Heteropyxis* is very different from Myrtaceae, especially in its *combination* of multiple pores, libriform fibers that are often septate, lack of vasicentric tracheids, distinctly heterogeneous vascular rays (often weakly heterogeneous to almost homogeneous in Leptospermoideae), and the lack of axial parenchyma.

Mature bark anatomy was studied in three samples of *Heteropyxis natalensis* (vouchers cited previously). The living inner bark is fairly thick (up to 15 mm). A relatively thin inner bark (±5 mm) is characteristic for many Myrtoideae (Roth, 1981). The bark is unusual for Myrtaceae because sclerenchymatous elements are almost absent. Only very sparsely distributed vertical strands of sclereids (in the sense of Parames-





FIGURES 9–11. Wood structure of *Heteropyxis natalensis* Harv. (Heteropyxidaceae).—9. Transverse section showing some pores in radial multiples and wide rays.—10. Radial section showing libriform fibers with dark-colored septa.—11. Tangential section showing wide heterogeneous rays (all from *Robbertse 1150*, PRU). Scale line = 50 μm.

waran, 1980) were observed (= fiber sclereids of some authors, e.g., Bamber, 1962). Sclereids are also rarely present as single or clustered elements in the dilatation zone. Phloem fibers are absent. Druse crystals are abundantly present in chambered crystalliferous strands—a diagnostic character for Myrtaceae, amongst other families (Roth, 1981). These strands are arranged in concentric, 1–2-seriate tangential layers regularly alternating with 1–3-seriate layers of mainly axial phloem parenchyma. Tanniniferous substances are abundantly present in the axial and ray parenchyma cells—a feature characteristic for the bark of Myrtaceae. Periderm structure is also reminiscent of Myrtaceae. The phellem is stratified and consists of mainly uniserial layers of thin-walled phellem cells alternating with mainly uniserial layers of phelloids with thick lignified walls. The phelloderm is parenchymatous and ±10 cell layers thick. No junction complexes were found between sieve tubes as has been reported by Tippett & Hill (1984) in certain Leptospermoideae. Secretory cavities are absent from the bark. Little seems to be known about bark construction in Lythraceae and most other families of Myrtales. A meaningful evaluation of the systematic significance of the bark anatomy of *Heteropyxis* was not possible due to a lack of comparative data. With the exception of the sparse sclerenchymatous elements and relatively thick inner bark, it agrees well with the general bark anatomy of Myrtaceae.

Pollen morphology. The pollen grains of *Heteropyxis* are typical of Myrtaceae (Erdtman, 1952, 1969; Fernandes, 1971; Schmid, 1980; Patel et al., 1984) and are more or less different from those of Lythraceae, Crypteroniaceae, Rhamnaceae, and Rutaceae (Erdtman, 1952). Grains of the possibly related genus *Psiloxylon* are also clearly myrtaceous (Schmid, 1980).

Embryology and seed. The embryology of *Heteropyxis* (H. Tobe & P. Raven, pers. comm. and 1987c) conforms to the basic embryological criteria defining the order Myrtales (cf. Tobe & Raven, 1983a). It differs from Myrtaceae particularly in having a bisporic, *Allium*-type embryo sac, and in some details of anther morphology. With the exception of *Alzatea* Ruiz & Pavon (Alzateaceae), all other Myrtales examined to date have the *Polygonum*-type of embryo sac formation. According to Tobe & Raven (pers. comm. and 1987c), embryological evidence strongly supports a subfamily (under Myrtaceae) or separate family status for *Heteropyxis*.

Chromosome number. Fernandes (1971) reported a chromosome count of $2n = 24$ in *Heteropyxis natalensis*. More recently, Johnson & Briggs (1984) recorded $2n = 24$ in *Psiloxylon mauritianum* (Hook. f.) Baill. A base number of $x = 11$ has been found in nearly all Myrtaceae studied (Atchison, 1947; Federov, 1969; Rye, 1979). Dysploid rises to $n = 12$ have been reported in a few species of Myrtaceae (see Rye, 1979). Cytological evidence is weak evidence for the relationships of *Heteropyxis* since a base number of $x = 12$ is also known in some Rhamnales (Raven, 1975) and $2n = 24$ ($x = 8$?) in some Lythraceae (Schmid, 1980). In *Heteropyxis*, Fernandes (1971) found a conspicuous satellite in one of the chromosomes.

Phytochemistry. Phytochemical evidence for *Heteropyxis* is scanty. The essential oils in two samples of dried leaves of *H. natalensis* were studied by Gouveia et al. (1972). Among the various substances identified was a fairly high yield of cineole (4.4–9%) and linalol (20%). According to Dahlgren & Thorne (1984), phloroglucin derivatives of the baeckerol, eugenin, and tasmonol types are characteristic of myrtaceous oils. The composition of essential oils generally does not provide very useful taxonomic evidence. Similar constituents may occur widespread in the plant kingdom and in taxa obviously not closely related. Matters may also be complicated by considerable variation in the essential oil composition of the same species due to seasonal and genetic variation (chemical races). Certain constituents nevertheless tend to dominate in the oils of particular taxa, and this may be taxonomically helpful. Returning to the essential oils of *Heteropyxis*, cineole (also known as eucalyptol) is a principal constituent of many *Eucalyptus* (Myrtaceae) oils (Penfold & Willis, 1961). It is also common in oils of *Melaleuca* L., *Artemisia* L., and *Lavendula* L. (Pollock & Stevens, 1965). Linalol, which seems to be the principal compound in *Heteropyxis* oil, is particularly common in oils from members of the Rutaceae, Apiaceae, Rosaceae, Lamiaceae (lavender oil), Lauraceae, and many others (Pollock & Stevens, 1965; Runeckles & Mabry, 1973; Karrer, 1976). It is relatively rare but not unknown in Myrtaceae.

Conclusions and relationships. In a phylogenetic analysis by Johnson & Briggs (1984) based on a large number of characters drawn from various fields, the Myrtaceae, Psiloxylaceae, and Heteropyxidaceae emerge as a distinct assemblage reflecting a high level of character state congruence. They conclude that both Heteropyxidaceae and Psiloxylaceae are relics that can reasonably be treated as families. Both probably separated early from the main myrtalean line, perhaps before the origin of Myrtaceae.

Available evidence indicates that Heteropyxidaceae are a clearly circumscribed family showing a unique combination of character states. Taken separately, many of these features can be found in Lythraceae and Myrtaceae. It is suggested that *Heteropyxis* represents the end of an evolutionary line rooted in the ancestral stock from which Lythraceae and Myrtaceae originated. Through parallel evolution it acquired various features also present in both the Lythraceae and Myrtaceae. Whether Heteropyxidaceae are closest to Lythraceae or Myrtaceae is unimportant; what counts is that all three families probably had a close connection in the distant past. It is nevertheless tempting to claim a perhaps closer affinity to Lythraceae. Whether *Psiloxylon* from Mauritius also belongs in Heteropyxidaceae must await further study.

Oliniaceae

Arnott ex Sonder in Harvey & Sonder

Description. Evergreen shrubs or trees up to 25 m high; bole often fluted and buttressed; mature bole bark more or less rectangularly fissured and scaley, sometimes with a reddish or yellowish pigment, inner bark usually strongly almond smelling; young leafy branchlets quadrangular, often tinged with red. Leaves opposite or rarely ternate, simple, petiolate, with rudimentary stipules, often smelling of almonds when crushed; lamina obovate, elliptic or lanceolate, often acuminate, entire, coriaceous, glabrous or minutely puberulous; venation brochidodromous, midrib usually terminating in a minute (glandular?) thickening. Inflorescence paniculate with the branches ending as 3-flowered cymules, terminal, or axillary and then usually much shorter than the subtending leaf; bracts opposite, as long as or shorter than the flowers, often caducous. Flowers basally subtended by a short internode ending with some blunt teeth, hermaphrodite, actinomorphic, (4–)5-merous, epigynous, scented, nectariferous. Hypanthium tubular, prolonged above the ovary, truncate or obscurely and minutely 5-toothed, ultimately deciduous. Calyx lobes (4–)5 on the rim of the hypanthium, conspicuous, and sometimes interpreted as petals, more or less linear-spathulate, or obovate-spathulate, white or pinkish, usually pubescent at the base, valvate, not enclosing the petals in bud. Petals (4–)5, inserted at the throat of the hypanthium tube, scalelike, alternating with, and much shorter than, the sepals, incurved and closing the tube in bud, spreading and reflexed at anthesis exposing the stamens, valvate, usually pink to crimson, pubescent. Stamens (4–)5, inserted on the inner rim of the hypanthium below the petals, incurved in bud; filaments very short, erect at anthesis, not exserted and with the anthers almost filling the mouth of the hypanthium tube; anthers dorsifixed, not versatile, 2-thecate, 4-sporangiate, connective thickened, introrse, longitudinally dehiscent. Pollen grains shed as monads, bright yellow and clumping together when fresh. Ovary inferior, (3–)5-locular; with (2–)3 superposed ovules per locule; ovules campylotropous, hypotropous; placentation axile; style simple, not exserted, and reaching the level of the anthers at anthesis, terete; stigma capitate. Fruit drupaceous, globose or ovoid, pink to bright red when ripe, marked by a circular scar left by the deciduous hypanthium; pericarp with the fleshy part edible and bittersweet, often almond tasting, endocarp tough and woody, longitudinally ribbed. Seeds usually one per locule and nearly always only one per fruit, ovoid ellipsoid or more or less subtrigonous, brown, without endosperm; embryo with a short radicle and two unfolded, spirally twisted or convolute cotyledons, oily.

General information. Oliniaceae are a monogeneric family of probably not more than eight closely related species of evergreen shrubs and trees endemic to southern and eastern Africa. *Olinia ventosa* (L.) Cufod. on St. Helena is most probably an introduction from South Africa (Cufodontis, 1960). *Olinia radiata* J. Hofmeyr & Phill. is one of the largest trees in some forests of Natal and Transkei, whereas *O. ventosa* is often a pioneer of forest margins, in particular the southern Cape. Both species produce a durable and handsome wood that has been exploited in the past (Von Breitenbach, 1965).

Treatment in the literature. Floral morphology in particular prompted some earlier workers

to relate Oliniaceae with Thymelaeaceae (e.g., Engler, 1897; Diels, 1936)—a family now excluded from the Myrtales (Dahlgren & Thorne, 1984). All recent systems of classification associate Oliniaceae with the Myrtalean families (Takhtajan, 1980; Cronquist, 1981; Dahlgren, 1983; Thorne, 1983). Dahlgren & Thorne (1984) included Oliniaceae among their families of "core" Myrtales. The placement of Oliniaceae in the Cunoniales (Hutchinson, 1959, 1967, 1973) has not gained support. In recent years, evidence from pollen morphology and embryology especially has provided useful data concerning its possible family relationships.

Macromorphology. As in many other Myrtales, rudimentary stipules are present in Oliniaceae (Weberling, 1963). These structures are also present in the putative related families Lythraceae, Punicaceae, Penaeaceae, and Crypteroniaceae but are rare in Melastomataceae (only in a few Memecyloideae) (Weberling, 1984). Rudimentary stipules are also present in Rhynchocalycaceae (Graham, 1984).

A generally neglected character is the presence or absence of a "glandular" leaf tip. The midvein of the lamina terminates in a "glandular" swelling or mucro in Oliniaceae, Rhynchocalycaceae, some Penaeaceae (e.g., *Sarcocolla* Boehm.), Punicaceae, and a few Lythraceae (*Galpinia* N. E. Br., *Lafoënsia* Vand.). The gland is unusually well developed in *Galpinia transvaalica* N. E. Br. and occurs subapically on the lower lamina surface. In this species it sometimes secretes a sweetish liquid that attracts large numbers of honeybees. A survey of "glandular" leaf apices in Myrtales may yield useful comparative data (see e.g., Rao & Chakraborti, 1982; Turner & Lersten, 1983).

Flowers of *Olinia* Thunb. were interpreted mainly in two different ways. The five conspicuous spreading lobes inserted on the upper rim of the hypanthium were regarded as petals, and the five scalelike structures just above the insertion of the five stamens as scales (e.g., Hofmeyr & Phillips, 1922; Rao & Dahlgren, 1969; Verdcourt, 1978). An alternative view is that the former lobes represent the calyx and the scales are the true petals (Dahlgren & Thorne, 1984). The latter interpretation is adopted in the present account.

In the immature flower (flower buds) the petals are incurved over the anthers and their margins fit tightly together, thereby effectively closing the mouth of the hypanthium. The calyx lobes spread out at an early stage and never really protect the flower bud. The protective function in flower buds in *Olinia* is therefore performed primarily by the petals. Some authors have obviously taken the flowers with incurved petals as mature, whereas they are in reality only buds. Anthesis takes place when the petals fold out or shrivel, thus exposing the stamens and allowing access to the nectar in the base of the hypanthium.

The recurved petals can be quite colorful (often deep pink) and are, at least in some species (e.g., *O. emarginata* Burt Davy), clearly petal-like. Floral biology of *O. ventosa* (= *O. cymosa* Thunb.) was studied in detail by Phillips (1926a) and is probably fairly representative for the family.

Although fairly small, the initial incurved position of the petals in Oliniaceae is matched by the petals in the buds of *Rhynchocalyx* Oliv. (Rhynchocalycaceae) and some species of Lythraceae (e.g., *Galpinia transvaalica* and species of *Lagerstroemia* L.). Despite their almost sessile nature, the stamens of *Olinia* are inflexed in bud thereby resembling Rhynchocalycaceae, Lythraceae, some Penaeaceae (*Endonema* A. Juss.), and many other families of the Myrtales. In some specimens of *Olinia* five minute teeth or lobes alternate with the large calyx lobes. These lobes were taken as reduced calyx by some of those who considered the large calyx lobes to be petals. These lobes (rarely present in material examined) seem to resemble the more or less well-developed appendages usually present in the sinuses of the calyx lobes in Lythraceae.

The flowers of *Olinia* are obhaplostemonous and in this respect agree with those of Rhynchocalycaceae, some Lythraceae (e.g., *Galpinia*), Alzateaceae, Crypteroniaceae, and Penaeaceae (stamens actually alternisepalous in the latter family because it has no petals). Ovular vascular supply in Oliniaceae is of the derived transeptal type (axial in most Myrtales) (Rao & Dahlgren, 1969; Schmid, 1984). A transeptal ovular supply also variously occurs in Punicaceae, Rhynchocalycaceae, and the more distantly related Onagraceae and Thymelaeaceae (the latter excluded from Myrtales by Dahlgren & Thorne, 1984) (Schmid, 1984).

Flowers of *Olinia* are often galled, resulting in a number of characteristic morphological features (Hofmeyr & Phillips, 1922; Cufodontis, 1960; Phillips, 1926a; Verdcourt, 1978). Although no distinct disc is present in normal flowers, copious nectar is secreted by the tissue sur-

rounding the base of the style. In *O. ventosa* honeybees were shown to be the chief pollinating agents. Sunbirds (Nectariniidae) rarely visited the flowers and then mainly to feed on the insect larvae in galled flowers. Fruit dispersal is aided by birds, monkeys, baboons, wild pigs, fruit bats, and elephants (Phillips, 1926a; Von Breitenbach, 1965). The pericarp remains succulent for a long time after the ripe drupes of *O. ventosa* have dropped to the ground. It takes from three to five months under dry, exposed conditions and from six to nine months in moist protected localities for them to shrivel. The shrivelled pericarp may persist for another 3–18 months before decaying (for more details on the biology of the flowers and fruits, see Phillips, 1926a).

Anatomy. Mújica & Cutler (1974) reported the presence of terminal sclereids in the leaves of Oliniaceae (not observed by Keating, 1984). This type of sclereid is also common in Melastomataceae (including Memecylaceae) but apparently absent in other Myrtales (Rao & Das, 1979). Diffuse sclereids are also present in Oliniaceae and the putative related Penaeaceae, Rhynchocalycaceae, Crypteroniaceae, Alzateaceae, Combretaceae, as well as in many other Myrtalean families.

Like all families of the Myrtales, Oliniaceae have intraxylary phloem and vestured pits (Van Vliet & Baas, 1984). In wood anatomy, Oliniaceae are closer to Lythraceae than Penaeaceae (Baas & Zweypfenning, 1979; Carlquist & Debuhr, 1977).

Pollen. *Olinia* pollen is heteropolar with one pole colpate and the other heterocolpate (Patel et al., 1983, 1984; pers. obs.). The pseudocolpi are restricted to one polar face only and are called half pseudocolpi (or half subsidiary colpi). Similar grains are not known elsewhere in Myrtales or the flowering plants. However, grains with regular pseudocolpi are also present in Lythraceae, Penaeaceae, Melastomataceae, Crypteroniaceae, Rhynchocalycaceae, and Combretaceae but are absent or indistinct in some Lythraceae and absent in Punicaceae (Patel et al., 1983; Dahlgren & Thorne, 1984). Its distribution in Myrtales appears to be taxonomically significant (Dahlgren & Thorne, 1984; Patel et al., 1984).

Embryology. Tobe & Raven (1983a, 1984a) identified a set of embryological features that clearly defines the Myrtales including Oliniaceae. In addition, Oliniaceae are characterized by having an ephemeral endothecium, campylotropous ovules and a relatively thick (3–5-layered) outer integument. An unusual feature is that the microsporogenous tissue is rarely partitioned by tapetal cells (Mauritzon, 1939; Tobe & Raven, 1984a). Only the ephemeral endothecium appears to have particular systematic significance. Tobe & Raven's claim that embryological features in Oliniaceae do not support a close relationship with any other member of the order is weakly based. An ephemeral endothecium also occurs in Crypteroniaceae (Tobe & Raven, 1983b, 1987a, 1987b), Alzateaceae (Tobe & Raven, 1984b), Rhynchocalycaceae (Tobe & Raven, 1984d), and Penaeaceae (Tobe & Raven, 1983a, 1984c). The presence of an ephemeral endothecium may be indicative of a common ancestry for these families.

Chromosome number. Chromosome numbers are $2n$ = ca. 40(–42) for *Olinia emarginata* and n = ca. 30(–28) for *O. radiata* (Goldblatt, 1976). The base number is probably $x = 10$, and polyploidy is clearly present. For the Penaeaceae Dahlgren (1968, 1971) reported $n = 10$. The base number of Rhynchocalycaceae is also $x = 10$ ($2n = 20$) (Goldblatt, 1976). Raven (1975) indicated a base number of $x = 8$ for Lythraceae, but $x = 10$ does occur in a few genera.

Phytochemistry. Specimens of *Olinia* can usually be readily identified in the field by the distinct almond smell of crushed leaves, twigs, and freshly cut bark and sapwood (Hofmeyr & Phillips, 1922). In at least *O. ventosa* the ripe pericarp and flowers (nectar) also smell of almonds (Phillips, 1926a, 1926b). Leaves from a herbarium specimen of *O. ventosa* were shown to contain the phenylalanine-derived cyanogenic glycoside, prunasin (Fikenscher & Hegnauer, 1977). However, cyanophoric constituents occur very erratically in vascular plants and seem to be an independently acquired attribute in various related and unrelated families (Hegnauer, 1977). Lythraceae, Memecylaceae, and Combretaceae are seldom cyanogenic (Cronquist, 1981), but data on this feature in the other families thought to be related to Oliniaceae is too scanty to permit any meaningful comparison at this stage.

No fructose oligosaccharides and fructans were detected in Oliniaceae (*O. ventosa*), Melastomataceae, Myrtaceae, Combretaceae, and Ona-

graceae (Pollard & Amuti, 1981). Data on other related families are not yet available. Aluminum was not accumulated in three species of *Olinia* that have been tested (Chenery, 1948). Aluminum is accumulated by at least some members of Crypteroniaceae, Rhynchocalycaceae, Memecylaceae, Combretaceae, and Myrtaceae (Chenery & Sporne, 1976; Chenery & Metcalfe, 1983).

Fungal parasites. The fungus *Asterina reticulata* Kalchbr. & Cooke emend. Doidge is apparently confined to species of *Olinia* (Doidge, 1950; Gorter, 1981) but, as pointed out by Thorne (1979), narrow host-specific parasites can obviously offer no clues to family relationships.

Conclusions and relationships. In a cladistic analysis of Myrtales (Johnson & Briggs, 1984) the Oliniaceae figure as a well-marked family associated with the Penaeacean assemblage (Alzateaceae, Rhynchocalycaceae, Penaeaceae, Oliniaceae, and perhaps Crypteroniaceae) and in particular the Penaeaceae. Their study indicates a more remote affinity with a broadly defined Lythraceae (including Sonneratiaceae and Punicaceae).

The totality of available evidence clearly indicates a close affinity between Oliniaceae, Alzateaceae, Rhynchocalycaceae, Crypteroniaceae, and Penaeaceae. There is strong evidence that these families may share a common ancestry. Penaeaceae, despite their rather different type of embryo sac, appear to be especially close to Oliniaceae. There are also signs of a link with a few woody genera currently included in Lythraceae and Punicaceae.

Penaeaceae Guillemin

Description. Glabrous shrubs and shrublets, rarely small trees, varying from low and decumbent to erect, to >2 m tall but mostly <60 cm. Branching sympodial or (*Endonema* A. Juss.) monopodial. Young branches often with distinct ridges ending on each side of the leaf bases as a short tip. Leaves opposite, decussate, simple, entire, linear to broadly ovate, obtuse or usually pointed, basically sessile but sometimes with tapering leaf base, often coriaceous, flat or longitudinally ridged, clear or dark green to glaucous, sometimes with thickened margins. Stipules small, each divided into a small row of fingerlike or (rarely) hairlike, multicellular, and secretory structures in the leaf axil. Inflorescence terminal or on lateral short shoots (rarely), a panicle, thyrse, "spike" with a terminal flower or indeterminate spike, or reduced to the terminal flower only. Flowers when terminal subtended by two or more pairs of bracteoles, when lateral generally by one pair of prophylls only. Supporting leaves of flowers similar to (often larger than) foliage leaves or (especially the upper) sometimes bracteose; prophylls generally narrower than these and often pale and ± bracteose. Flowers bisexual, actinomorphic, apetalous, 4-merous, with a variably long floral tube (hypanthium) with stamens inserted in the mouth. Floral tube pale yellowish, yellow-green, pink, purple, crimson, or rarely bright yellow. Lobes ovate to triangular, valvate or reduplicate-valvate, generally acute, of same color as floral tube. Stamens 4, alternating with sepal lobes; filaments narrow, erect, from much shorter than anthers to longer than these; anthers with ovoid to cubic, fleshy connective, 2-thecate, 4-sporangiate; sporangia introrse, from as long as the connective to less than half its length, often distant from each other basally, with thin, whitish sporangial walls. Pollen grains dispersed singly. Disc lacking. Pistil with superior, 4-locular, often 4-lobate ovary and a terminal style, this narrow and subterete (as in *Endonema*) to stout and with 4 longitudinal commissural ridges (*Stylapterus* A. Juss.) or prominent wings (*Penaea* L.) running from ovary septa to the squarish, truncate style apex; stigma capitate or 4-lobated on the apex of a narrow style, or divided into four stigmatic areas in the corners of the apex of the stylar wings. Ovules 2–4 per locule, either all inserted basally or (*Glischrocolla* (Endl.) A. DC., *Endonema*) inserted centrally and in the mid part of the locules; each locule with one ascending and one pendulous ovule. Fruit a firm, often hard, loculicidal capsule. Seeds elongate, almost exendospermous; embryo straight, with small cotyledons.

General information. Penaeaceae consist of seven genera, all confined to the Cape Province and concentrated in the southwest. *Penaea* has the widest distribution towards the east, extending from the Cape Peninsula to Port Elizabeth, but not beyond the Worcester District in the northwest. Most species grow on mountain slopes, sometimes (*Sonderothamnus petraeus* (Barker) Dahlgr.) in crevices of vertical rocks. Generally the substrate is sand weathered from T.M.S.

Treatment in the literature. Penaeaceae in the past have generally been placed in either Myr-

tales or Thymelaeales, the latter sometimes included in Myrtales. Outlines of the literature are given in the revisions of the genera by Dahlgren (1967–1971). The family is fairly well known and has been the subject of detailed studies of wood anatomy (Carlquist & De Buhr, 1977), vegetative anatomy in general (Van Vliet & Baas, 1984), embryology (Stephens, 1910; Tobe & Raven, 1984), and pollen morphology (Patel et al., 1984). The relationships of the family have been discussed by Dahlgren & Thorne (1984), Johnson & Briggs (1984), in relation to Alzateaceae by Graham (1984), and in relation to Rhynchocalycaceae here. In all the publications since 1960, including the classifications of Melchior (1964), Takhtajan (1980), Cronquist (1981), Thorne (1981, 1983), and Dahlgren (1980, 1983), there is complete agreement that Penaeaceae belong in Myrtales. The classification of Thymelaeaceae in (or with) this order is still not settled. It is also clear that the position of Penaeaceae within Myrtales is among families with colporate-heterocolpate pollen grains, i.e., pollen grains where the true apertures alternate with pseudocolpi (subsidiary colpi, colpoid "rugae").

Anatomy. The presence of internal phloem and vestured pits (found in virtually all Myrtales) contributes in confirming the position of Penaeaceae in Myrtales. Carlquist & De Buhr (1977) and Van Vliet & Baas (1984) give further evidence for relationship of Penaeaceae especially to Memecylaceae, Crypteroniaceae, and Melastomataceae. In most of the anatomical characteristics reviewed by Van Vliet & Baas (1984), Penaeaceae stand out as relatively unspecialized within the order.

Pollen morphology. Patel et al. (1984), describing the pollen grains of Penaeaceae, found a great variation in number and length of apertures (short in, for example, *Glischrocolla,* long and sometimes syncolpate in *Penaea* and *Stylapterus*), position of endoapertures, and surface (rugulate-psilate). Exomorphologically, Patel et al. (1984) found that Penaeaceae pollen grains agree best with those in Oliniaceae, Memecylaceae, Melastomataceae, and Combretaceae; endomorphologically with those in Oliniaceae. There is also some similarity to the pollen grains in Rhynchocalycaceae.

Embryology and seed. Since Stephens's (1910) now classical study of the embryology of Penaeaceae, in which she discovered the 4-sporangiate, 16-nucleate *Penaea* type embryo sac, the family has been further studied by Tobi & Raven (1984). They confirmed the findings of Stephens and reported some additional characteristics, notably the ephemeral endothecium, which is undoubtedly derived and shared with Oliniaceae, Rhynchocalycaceae, Alzateaceae, and Crypteroniaceae. The *Penaea*-type embryo sac is unique to the family. *Alzatea* (Alzateaceae) and *Rhynchocalyx* (Rhynchocalycaceae) further differ from the Penaeaceae by having a multicellular archesporium in the ovule and the micropyle formed only by the inner integument. *Rhynchocalyx* also has a nonfibrous extegmen in the seed. Oliniaceae differ from the Penaeaceae in having campylotropous ovules and a 3–5-layered outer integument. Tobi & Raven (1984) reported variation in the testal layer of the seed coat in *Penaea* and *Saltera* Bull., but in both genera the two tegminal layers are fibrous.

Chromosome numbers. The basic chromosome number in Penaeaceae is $x = 10$ (Dahlgren, 1968), in which Penaeaceae agree with Oliniaceae and Rhynchocalycaceae (Goldblatt, 1976).

Phytochemistry. Imperfectly known. Proanthocyanin has been reported for this family, as for Rhynchocalycaceae, Oliniaceae, and some Lythraceae (R. Patterson, pers. comm.; see also discussion under Rhynchocalycaceae).

Conclusions and relationships. Penaeaceae are related to a distinct group of families of Myrtales characterized by most or all of the following characteristics: entire, opposite leaves; small stipules in axillary rows; foliar sclereids; valvate calyx teeth; one single staminal whorl opposite the sepals (obhaplostemony); a distinctive hypanthium with stamens inserted on its rim; anthers with a well-developed, often fleshy connective body; pollen sacs with ephemeral endothecium; and pollen grains with apertures alternating with pseudo colpi.

This group of families includes (some exceptions of the mentioned characteristics are admitted) Memecylaceae, Crypteroniaceae, Penaeaceae, Oliniaceae, Rhynchocalycaceae, and Alzateaceae. Some members of this group are similar in several characters to Lythraceae or Melastomataceae, or both. Penaeaceae have great similarities to all the families of the group mentioned above but is not conspicuously allied to any of them. In a cladistic study Johnson & Briggs (1984) placed Penaeaceae and Oliniaceae in the

same clade, having as synapomorphies lack of apotracheal parenchyma, loss of trilacunar nodes, and reduction of stamen filaments. These synapomorphies are dubious in our view: presence of apotracheal parenchyma, see Van Vliet & Baas (1984); trilacunar nodes are probably not primitive in the order; filaments are often well developed and are even long in some Penaeaceae, e.g., in *Saltera* (see Dahlgren, 1968, fig. 19). Nevertheless, the two families seem to be closely related to each other and have in common essentially the same pollen morphology (see earlier text), a shared basic chromosome number (x = 10), and the southern African concentration in distribution. Epigyny, presence of petals, and embryological details are different. The great similarities between Rhynchocalycaceae and Penaeaceae will be discussed under the treatment for Rhynchocalycaceae.

Penaeaceae probably diverged rather early from an ancestral group related to early Lythraceae sensu lato. Its close relationships to each of Memecylaceae, Crypteroniaceae, and Alzateaceae, and especially Oliniaceae and Rhynchocalycaceae are more or less clear, although an evaluation of the detailed relationships cannot be done here.

Rhynchocalycaceae Johnson & Briggs

Evergreen trees up to 12 m high, young shoots terete or slightly oval in transection, glabrous. Leaves simple, opposite, decussate; on actively growing coppice shoots relatively large, virtually sessile with the lamina base rounded, cordate to amplexicaul; on mature growth smaller, petiolate, with the lamina tapering towards both ends; lamina entire, coriaceous, with a minute glandular(?) marginal thickening at the terminus of the midrib, usually drying yellowish green in herbarium specimens; venation weakly brochidodromous with a tendency towards eucamptodromous; stipules rudimentary, very small, lateral, marcescent. Inflorescence a multifloral panicle, mainly terminal; bracts usually caducous. Flowers white, bisexual, actinomorphic, hexamerous, tetracyclic; hypanthium short, patelliform, slightly perigynous. Sepals 6, white and petal-like, recurved, valvate and distinctly beaked in bud, persistent. Petals 6, inserted on the rim of the hypanthium and alternating with the sepals, conspicuously and narrowly clawed, recurved, fragile, and fugacious; limb more or less orbicular, margin lacerate, hoodlike and covering the anthers in bud only. Stamens 6, antepetalous, inserted near the inner rim of the hypanthium; filaments more or less terete; anthers sub-basifixed, versatile, 2-thecous, 4-sporangiate, introrse, longitudinally dehiscent; connective elliptical with lateral sporangia, inflexed in bud. Pollen grains dispersed separately. Disc absent. Ovary bilaterally compressed, superior 2(–3)-locular; style stout, shorter than the ovary, basal part persistent; stigma capitate, covered by minute papillae; ovules ca. 15–20 per locule, anatropous, pleurotropous, superposed in a single vertical series; placentation axile. Fruit a dorsiventrally compressed (rarely trigonous) capsule, loculicidal at the apex, reddish brown. Seeds ca. 15–20 per locule, depressed-ovoid, narrowly winged (expanded raphe); testa thin and papery, rather smooth, brownish, without endosperm; embryo more or less flattened, cotyledons folded inside.

General information. *Rhynchocalyx lawsonioides* Oliv. is an extremely rare evergreen tree endemic to the sandstone (Natal Group; previously known as Table Mountain Sandstone) region of southern Natal and Pondoland. First collected in 1884, it was only rediscovered in 1966 (Strey & Leistner, 1968). It grows mainly on forest margins, often near water courses.

Treatment in the literature. Oliver (1894) first described the species and assigned it to Lythraceae. Although excluded from Lythraceae by Koehne (1903), Sprague & Metcalfe (1937) endorsed its placement in Lythraceae, close to *Lagerstroemia* L. and particularly *Lawsonia* L., with which it agrees in a number of morphological and anatomical characters.

Van Beusekom-Osinga & Van Beusekom (1975) included *Rhynchocalyx* and *Alzatea* Ruiz & Pavon in subfamily Alzateoideae of their expanded Crypteroniaceae, *Rhychocalyx* constituting the monospecific tribe Rhynchocalyceae. This treatment (also Van Beusekom-Osinga, 1977) has not met with wide support. On embryological grounds Tobe & Raven (1984d) suggested that *Rhynchocalyx* should perhaps be placed in a separate family, and Johnson & Briggs (1984) formally described the family Rhynchocalycaceae. Rhynchocalycaceae are maintained by Dahlgren & Thorne (1984), who consider it well placed in Myrtales. A very useful comparison of *Rhynchocalyx* and associated genera is provided by Graham (1984). It shares an im-

pressive number of features with *Alzatea* (Alzateaceae).

Macromorphology. The foliage leaves of *Rhynchocalyx* are opposite and provided with two minute (rudimentary) stipules situated on either side of the leaf axil at the base of the petiole. They resemble the rudimentary stipules in some woody members (e.g., *Galpinia* N. E. Br., *Lagerstroemia, Lawsonia*) of Lythraceae (rudimentary intrapetiolar stipules are general of Lythraceae). Rudimentary stipules are present in many other Myrtales, including the putative related Punicaceae, Oliniaceae, Penaeaceae, and Crypteroniaceae (Weberling, 1984).

As pointed out under Oliniaceae, the midvein of the lamina terminates in a minute "glandular" mucro in *Rhynchocalyx*. A "glandular" leaf apex is also present in Oliniaceae, Punicaceae, at least some Penaeaceae (e.g., *Sonderothamnus* R. Dahlg., *Saltera* Bullock), and in a few woody Lythraceae (e.g., *Sonneratia* Comm. ex Endl., *Capuronia* Lourteig, *Galpinia, Lafoënsia* Vand.).

A peculiar feature of *Rhynchocalyx* apparently not previously recorded is the presence of leaf dimorphism. Leaves on actively growing coppice shoots differ conspicuously from the leaves on mature growth in being virtually sessile and much larger, with the lamina base rounded, cordate or even tending to be amplexicaul.

Rhynchocalyx agrees with Penaeaceae in the obhaplostemonous flowers and insertion of stamens almost on the hypanthium rim (Dahlgren & Thorne, 1984). Obhaplostemonous flowers are also encountered in some Lythraceae, and this is the prevailing condition in Oliniaceae, Alzateaceae, and some Crypteroniaceae (one diplostemonous whorl in *Axinandra* Thw.). Although the stamens in Lythraceae are usually inserted fairly low on the inside of the hypanthium, the nearly marginal insertion in *Rhynchocalyx* does not refute a Lythraceous affinity. Stamens inserted near the rim of the hypanthium occur for example in *Lawsonia*. Dahlgren & Thorne (1984) described (and illustrated) the petals of *Rhynchocalyx* as hoodlike, and Van Beusekom-Osinga (1977) considered this one of the principal features upon which the Crypteroniaceae s.l. is based. Johnson & Briggs (1984) used the presence or absence of "hooded petals (*Rhynchocalyx* type)" as a character in their phylogenetic analysis of Myrtales. This interpretation is unacceptable. The unguiculate petals are bent inward over the strongly inflexed stamens only in bud. After anthesis the petals spread out and no longer cover the anthers. An almost identical state occurs in some Lythraceae, e.g., *Galpinia* and *Lagerstroemia*. These petals are in fact one of the main floral features of *Rhynchocalyx* strongly suggestive of a Lythraceous affinity. The mature ovary of *Rhynchocalyx* is bilocular (rarely trilocular) and not unilocular as described by Van Beusekom-Osinga & Van Beusekom (1975). Very young ovaries are unilocular, but these are subsequently rendered bilocular by an extension of placental tissue from opposite sides of the ovary wall (H. Tobe, pers. comm.). Graham (1984) also considered the ovary bilocular. The ovular vascular supply of *Rhynchocalyx* is transeptal, thereby recalling certain Myrtaceae, Punicaceae, Oliniaceae, and Onagraceae (Schmid, 1984).

Anatomy. Leaf, twig, and nodal anatomy of *Rhynchocalyx* indicate a closer affinity to some Lythraceae, Oliniaceae, and Melastomataceae than to other members of the Crypteroniaceae s.l. (Van Vliet & Baas, 1975). Leaf anatomy in particular agrees well with Lythraceae (Keating, 1984). Wood anatomy of *Rhynchocalyx* also shares similarities with Oliniaceae and particularly Lythraceae (Baas & Zweypfenning, 1979). Van Vliet & Baas (1984) included *Rhynchocalyx* in their general wood anatomical description of Lythraceae.

Sclereid idioblasts are present in the petiole and to a lesser extent in the lamina of *Rhynchocalyx* (Van Vliet & Baas, 1975). Foliar sclereids also occur in the Penaeaceae, Oliniaceae, Alzateaceae, Crypteroniaceae, Lythraceae (rare), and other myrtalean taxa (Rao & Das, 1979; Dahlgren & Thorne, 1984).

Pollen morphology. The pollen grains of *Rhynchocalyx* are characterized by the presence of three colporate apertures alternating with three pseudocolpi (Muller, 1975; Patel et al., 1984). Within Crypteroniaceae s.l. the grains of *Rhynchocalyx* are more or less similar to those of *Dactylocladus* Oliv. and *Axinandra* but rather different from the bisyncolpate grains of *Crypteronia* Blume and tricolpate grains of *Alzatea* (Muller, 1975; Patel et al., 1984). In Myrtales, heterocolpate pollen grains are also found in Lythraceae, Oliniaceae, Penaeaceae, Melastomataceae (incl. Memecyloideae), and Combretaceae (Patel et al., 1983, 1984; Dahlgren & Thorne, 1984). Pseudocolpi are lacking in *Galpinia* (Graham et al., 1985).

Embryology and seed. The embryology of *Rhynchocalyx* (Tobe & Raven, 1984d) agrees well

with the basic embryological features of Myrtales (Tobe & Raven, 1983a). It is rather different from *Axinandra* (Tobe & Raven, 1983b), *Crypteronia* (Tobe & Raven, 1987a), *Dactylocladus* (Tobe & Raven, 1987b), and *Alzatea* (Tobe & Raven, 1984b), although all five share an ephemeral endothecium, also recorded in Oliniaceae and Penaeaceae, and its presence may signify a common ancestry for these taxa (Tobe & Raven, 1984a, 1984c). Tobe & Raven (1984d) nevertheless considered *Alzatea* to agree more closely in its embryological features with *Rhynchocalyx* than with any other genus studied thus far. The presence of a multicelled archesporium in *Rhynchocalyx* recalls Lythraceae. Among myrtalean families this feature is only known in Alzateaceae and Lythraceae subfamily Sonneratioideae (Sonneratiaceae of some authors) (Tobe & Raven, 1984b, 1984d). *Rhynchocalyx* differs in several embryological features from Lythraceae, the most important of which is probably the ephemeral endothecium. An embryological comparison with *Galpinia* (Lythraceae), which shares some morphological features with *Rhynchocalyx,* does not support a close affinity between the two taxa (H. Tobe, pers. comm.).

In *Rhynchocalyx* the seed coat is derived from both the outer and inner integument (Tobe & Raven, 1984d). The exotegmen of the mature seed coat does not become tracheidal, whereas it characteristically does in Lythraceae, including *Galpinia* (H. Tobe, pers. comm.). The winged seeds of *Rhynchocalyx* are probably distributed by the wind, and the relatively thin seed coat may be an adaptation to facilitate this type of distribution.

Chromosome number. Goldblatt (1976) reported a chromosome count of $n = 20$ for *Rhynchocalyx.* Raven (1975) indicated $x = 8$ for most Lythraceae, but $x = 10$ does occur in a few genera. *Galpinia* has $2n = 16$ (Tobe et al., 1986). A base number of $x = 10$ is also likely for Oliniaceae (Goldblatt, 1976) and Penaeaceae (Dahlgren & Thorne, 1984).

Phytochemistry. Aluminum is accumulated in Crypteroniaceae (*Axinandra* and *Crypteronia*) and *Rhynchocalyx* (confirmed during the present study), a character of possible taxonomic significance (Chenery & Metcalfe, 1983). Aluminum accumulators are particularly common in Melastomataceae (Memecyloideae) but not yet recorded in Oliniaceae or Lythraceae (Chenery, 1948; Chenery & Sporne, 1976). Penaeaceae has apparently not been tested. Chenery & Sporne (1976) concluded that the phylogenetic significance of aluminum accumulation is doubtful, although statistical analysis suggests that the process itself is a primitive character. Proanthocyanin was recently detected in *Rhynchocalyx,* as well as some species of Penaeaceae, Oliniaceae, and Lythraceae (R. Patterson, pers. comm.), but is absent in *Lawsonia, Galpinia,* species of *Cuphea* (Lythraceae), and Punicaceae. The foliar flavonoids of *Rhynchocalyx* agree with the typical profile of Myrtales (Averett & Graham, 1984). Noteworthy is perhaps the absence of myricetin, which is frequently found in the order, but also lacking in *Alzatea* (Graham & Averett, 1984).

Conclusions and relationships. In the cladistic analysis of Johnson & Briggs (1984) *Rhynchocalyx* associates with the so-called Penaean assemblage (Alzateaceae (in particular), Oliniaceae, Penaeaceae, Rhynchocalycaceae, and perhaps Crypteroniaceae). The analysis does not support the suggested inclusion of *Rhynchocalyx* and *Alzatea* in Crypteroniaceae. *Rhynchocalyx* does not associate closely with Lythraceae despite their several shared features. However, some of the characters used in the cladistic analysis (e.g., characters 33, 34 & 35 are questionable). These characters tend to unjustly inflate the unique nature of *Rhynchocalyx,* an effect enhanced by the fact that the character states employed do not cover the range of variation within a taxon but only represent the state presumably ancestral within a group.

Rhynchocalyx is clearly related to a group of families consisting of Crypteroniaceae, Penaeaceae, Oliniaceae, Alzateaceae, Oliniaceae, and Lythraceae. However, it appears to be without particularly close living relatives. It is an ancient relic (almost extinct), endemic to the sandstone region of southern Natal and Pondoland—an area particularly rich in endemic species of woody plants, many of which appear to be relics of an ancient Gondwana flora. In addition, the flora of this center of endemism contains a stong present-day Cape element. The putative affinity between Rhynchocalycaceae and Penaeaceae, confined to the Cape region, is therefore of interest. Oliniaceae, Rhynchocalycaceae, and Penaeaceae seem to have evolved from the same ancestral stock, and this is to some extent also reflected by their present geographical distribution. Although Rhynchocalycaceae and Penaeaceae are also holoendemics because of their confinement to related sandstone formations, a link between

the now separated edaphic islands on which they occur could have been in existence before the breakup of western Gondwana.

Melianthaceae Link

Description. Evergreen subshrubs, shrubs or trees. Leaves alternate, petiolate, imparipinnate, occasionally with a winged rhachis; leaflets petiolulate or sessile, in two to several pairs, entire, serrate or deeply toothed, glabrous or hairy; stipules present, well developed, paired, either free and inserted laterally at the base of the petiole (some species of *Melianthus* L.) or laterally connate and intrapetiolar, persistent or deciduous. Inflorescence a raceme, terminal or axillary, dense or lax, sessile or peduncled, erect or pendulous, hermaphroditic (*Melianthus*) or polygamous (confirmed in at least some species of *Bersama* Fresen.); rhachis with flowers solitary of 2–4 per node; bracts well developed, with numerous sterile bracts surrounding the base of the inflorescence in one species of *Bersama.* Flowers bisexual in *Melianthus* (always?), bisexual(?), functionally female (with antherodes) or functionally male (with pistillodes) in *Bersama,* often resupinate by twisting of the pedicel in *Melianthus,* slightly to markedly zygomorphic, usually 4–5-merous, hypogynous. Sepals 5, sometimes 4 by union (or close coherence) of two, unequal, imbricate, free or basally connate, one of them spurred or saccate-gibbous in *Melianthus.* Petals 4–5, free, clawed, imbricate, conspicuous, and exserted or reduced to four in *Melianthus,* and in some species apically coherent by cilia and the twisting of the apices, usually partly or completely covered by hairs. Disc well developed, variously unilateral or rarely annular-pentagonal, producing copious nectar (particularly in *Melianthus*). Stamens 4–5(8), antisepalous, equal and basally monadelphous in *Bersama,* didynamous and free or sometimes with the two nearest the nectary basally connate in *Melianthus*; anthers dorsifixed, versatile, 2-thecate, 4-sporangiate, introrse, longitudinally dehiscent; antherodes smaller than the anthers, indehiscent and without pollen (*Bersama*). Pollen grains shed as monads, creamish-yellow when fresh. Ovary superior, sessile, often hairy, 4–5-locular, with basal (*Bersama*) or axile (*Melianthus*) placentation; ovules solitary (*Bersama*) or 2–4 per locule (*Melianthus*), anatropous, erect or pendulous; style simple, often hairy below, more or less persistent in *Melianthus*; stigma slightly or strongly capitate (*Bersama*) or indistinct (*Melianthus*); pistillodes smaller than the ovary, with vestigial ovules and lacking a stigma. Fruit a capsule, inflated in *Melianthus,* papery or coriaceous, longitudinally sulcate and sometimes apically lobed, usually with prominent venation, often pubescent, tardily loculicidally dehiscent, subglobose in *Bersama,* woody, smooth, rugose to densely echinate, dehiscing loculicidally by 4–5 valves. Seeds 1 or 2 per locule, usually few (1 or 2) per fruit and globose in *Melianthus,* black and shiny, exarillate, often distributed when the capsule is blown off by the wind, elliptic or elliptic obovate in *Bersama,* black or reddish, subtended by an often yellowish aril, at least in some instances distributed by birds; embryo straight, cotyledons flat and collateral; endosperm abundant, starchy or oily.

General information. Members of the genus *Melianthus* are herbaceous or soft-wooded subshrubs that are unpleasantly scented when bruised. Secondary growth is restricted, and there is essentially no increase in stem diameter in older shoots. The genus is endemic to southern Africa, often occurring in arid areas. Some species have been reduced to subspecific status (Tansley & Schelpe, 1984), bringing the number of species currently accepted to six.

Bersama constitutes about eight species of trees or shrubs, usually confined to forest regions in southern and tropical Africa. The leaves are not strongly scented. It is a taxonomically difficult group, with leaves from saplings often very different in shape, size, and indumentum from those on adult plants. The main center of the genus appears to be southern Africa, from whence it spread rapidly to the north (Verdcourt, 1950). Most of the tropical African material is assigned to the polymorphic *B. abyssinica* Fresen., with several subspecies and varieties (Verdcourt, 1956). There are about four species in southern Africa, of which at least two, *B. swinnyi* Phillips and *B. lucens* (Hochst.) Szyszyl., are very distinct.

Superficially *Bersama* and *Melianthus* are rather different (Table 2). Hence the common practice of classifying the two genera in the same family will also be dealt with later.

Treatment in the literature. In this account *Greyia* is excluded from Melianthaceae (see Greyiaceae). Despite earlier treatments including Melianthaceae in Sapindaceae (e.g., Hooker,

TABLE 2. Selected differences between the two genera of the Melianthaceae.

	Melianthus	*Bersama*
Habit	half-shrubs, herbaceous or subwoody	usually trees, occasionally shrubs, woody
Smell of crushed vegetative parts	unpleasantly scented	not unpleasantly scented
Stipules	lateral and free; intrapetiolar only in *M. major*	intrapetiolar, laterally connate
Floral sex and orientation	bisexual, resupinate	bisexual or unisexual (polygamous), not resupinate (at least in southern African species)
Sepals	one spurred or saccate gibbous	not spurred or saccate gibbous
Ovules	2–5 per locule	1 per locule
Placentation	± axile	± basal
Fruits	inflated papery capsules	tough-walled (often woody) capsules
Seeds	aril absent	aril present

1873; Gürke, 1896), the two families seem to be distinct. In modern systems of classification Melianthaceae is usually placed near Sapindaceae in the order Sapindales. Possible affinities with various other families, notably Zygophyllaceae (Radlkofer, 1890) and more recently Lardizabalaceae (Corner, 1976), have been suggested. However, Dahlgren (1983) pointed out that the presence of endosperm in the seed and the relatively small embryo make Melianthaceae somewhat anomalous in Sapindales. The conspicuous stipules and styloids are also not typical for the order.

Macromorphology. The conspicuous stipules in Melianthaceae are not typical for the Sapindales. These are often (not always) intrapetiolar (Guédès, 1979, preferred "median stipules"). Flowers of *Bersama* tend to be polygamous, a feature common in Sapindaceae, Anacardiaceae, and Hippocastanaceae. The extrastaminal and usually unilateral disc in Melianthaceae strongly suggests an affinity with the Sapindaceae. In Anacardiaceae the disc is usually intrastaminal and annular.

Some of the morphological differences between *Melianthus* and *Bersama* evidently reflect differences in adaptive radiation. Flowers of *Melianthus* are bird pollinated (Vogel, 1954), and they clearly display the syndrome associated with ornithophily (flowers are also visited by bees). The number of petals in *Melianthus* is reduced to four. Khushalani (1963) produced evidence suggesting that the nectariferous disc most probably represents a modified fifth petal. Some species of *Melianthus* produce a blackish nectar (e.g., *M. villosus* H. Bol.). The inflated fruits are wind distributed (Marloth, 1896). Little is known about the mode of pollination in *Bersama,* but floral structure does not suggest ornithophily (the red-flowered *B. rosea* Hoyle may be an exception). Seeds of *Bersama* are most probably distributed by birds, hence the presence of a brightly colored aril.

Anatomy. Perhaps the most striking anatomical feature is the presence of styloids in both *Bersama* and *Melianthus.* These are not only present in the vegetative parts, but sometimes also in the seed coat (Metcalfe & Chalk, 1950; Jackson & Jethwa, 1973; Corner, 1976). Among possible related taxa, styloids are rare in Sapindaceae and the perhaps more distantly related Rutaceae, Simaroubaceae, and Zygophyllaceae (Metcalfe & Chalk, 1950, 1983). Medullary bundles are known in Melianthaceae and Sapindaceae but apparently not in other Sapindales or Rutales. Septate fibers, recorded in the wood of *Bersama* (Heimsch, 1942), are common in both Sapindaceae and Anacardiaceae (Metcalfe & Chalk, 1950, 1983). Resin ducts (common in Anacardiaceae) and secretory cells (often present in Sapindaceae) are absent in Melianthaceae.

Other anatomical similarities between *Bersama* and *Melianthus* include the presence of multilacunar nodes (Metcalfe & Chalk, 1950; Hilger, 1978b), similar vasculature in the pinnately compound leaves (Hilger, 1978a), amphivasal medullary bundles (Metcalfe & Chalk, 1950), glandular trichomes in some species (Jackson & Jethwa, 1973; Hilger, 1978a), and presence of styloids in vegetative parts.

Pollen morphology. Erdtman (1952) studied pollen of *Bersama, Melianthus,* and *Greyia* (now in Greyiaceae) and concluded that pollen grains more or less similar to those in Melianthaceae s.l. occur in the Anacardiaceae and Rutaceae. According to Erdtman, grains in Geraniaceae, Sapindaceae, Staphyleaceae, and Zygophyllaceae are less similar or different. A recent comprehensive study of Sapindaceae pollen grains (Muller & Leenhouts, 1976) revealed forms not unlike those of Melianthaceae.

We are indebted to J. Praglowski for the following notes on the pollen grains of *Bersama* cf. *tysoniana* Oliv. (Fig. 12): grains isopolar, radially symmetrical, prolate (polar axis ca. 49 μm long, equatorial diameter ca. 36 μm), 3-colporate, colpi at equator often slightly narrower than in remaining parts, colpus membrane with minute processes, ora lalongate; exine structure lacking; exine sculpture rugulose.

Embryology and seed. Very few species are known embryologically (see summary by Davis, 1966), and there is considerable scope for more detailed studies. The endothecium in *Melianthus major* does not develop fibrous thickenings (Maheswari, 1950; Khushalani, 1963). This is rather unusual in Sapindales. Also unusual for the order are the reports that Melianthaceae pollen grains are shed in the trinucleate state (Brewbaker, 1967). However, *M. major* L. is reported elsewhere (Davis, 1966) to have binucleate grains. Pollen grains of *M. major* are claimed to be often sterile owing to aberrant nuclear divisions, and up to five nuclei per grain were recorded by Khushalani (1963). A reassessment of the nucleate state in Melianthaceae is necessary before any definite conclusions can be made.

The embryogeny of *Bersama transvaalensis* Turrill and *Melianthus major* has been studied in detail (Steyn, 1975, 1977; Steyn et al., 1986). Embryo development follows the *Penaea* variation of the Asterad type. In both species the embryo lacks a suspensor, and an epiphysis initial is formed. The globular tetrads and suspensorless embryos, as in Melianthaceae, are rare in the flowering plants (Johansen, 1950). Among sapindalean families, the *Penaea* variation of the Asterad type occurs in Anacardiaceae (Johansen, 1950) and a suspensor is also usually absent in this family (Davis, 1966). Young embryos very similar to those in Melianthaceae were described in various Anacardiaceae, e.g., monoembryonic varieties of *Mangifera* L. (Juliano & Cuevas, 1932; Juliano, 1937; Sachar & Chopra, 1957; U. R. Singh, 1960), *Pistacia* L. (Grundwag, 1976) and *Schinus* L. (Copeland, 1959). Unfortunately, embryo development has been investigated in very few species of Sapindaceae and other families of Sapindales, and a more meaningful comparison is not possible at this stage.

Steyn (1975, 1977) often found irregular and degenerated embryos in ovules of *Melianthus major.* She also recorded poor seed set in this species. Abnormal embryos and poor fruit (seed) development are also well known among cultivated species of Anacardiaceae, particularly *Mangifera* (see papers cited in the previous paragraph) and *Pistacia* (Grundwag, 1976).

The unilocular ovary with one basal ovule in *Mangifera* (as hitherto depicted in illustrations) superficially appears rather similar to a *Bersama* ovary reduced to one locule. According to Sharma (1954) the floral vascular anatomy in *Mangifera* suggests that the monocarpellary condition appears to have been derived from a tricarpellary state. However, a recent re-evaluation of the structure of the ovule in *M. indica* L. shows that it differs considerably from the state in *Bersama,* thereby dismissing any suggestion of a close affinity between the two taxa (Robbertse et al., 1986).

The testa in seeds of Melianthaceae develops from a multiserial outer integument and is multiplicative and mainly unlignified. The outer epidermis is transformed into a macrosclereid layer in *Melianthus* (an adaptation to its generally arid environment?) but not in *Bersama.* The inner integument is crushed (Guérin, 1901; Corner, 1976; Steyn, 1977). Similar testas also occur in Sapindaceae (Guérin, 1901; Magen, 1912). Corner (1976) concluded that the seeds of Melianthaceae do not have the Sapindaceae structure (we claim the contrary). He suggested an affinity with seeds of the Lardizabalaceae, which does not in other features seem to be closely allied to Melianthaceae. In Anacardiaceae the presence of an endocarp results in rather unspecialized seed coats that do not provide criteria useful for comparison with other families (Corner, 1976).

Seeds of Melianthaceae are albuminous (Magen, 1912; Corner, 1976; Steyn, 1977), a condition anomalous in Sapindales, although considerable endosperm also occurs in Staphyleaceae. A few layers of perisperm persist in the mature seed of *Bersama* (Steyn, 1977).

Chromosome number. Known chromosome

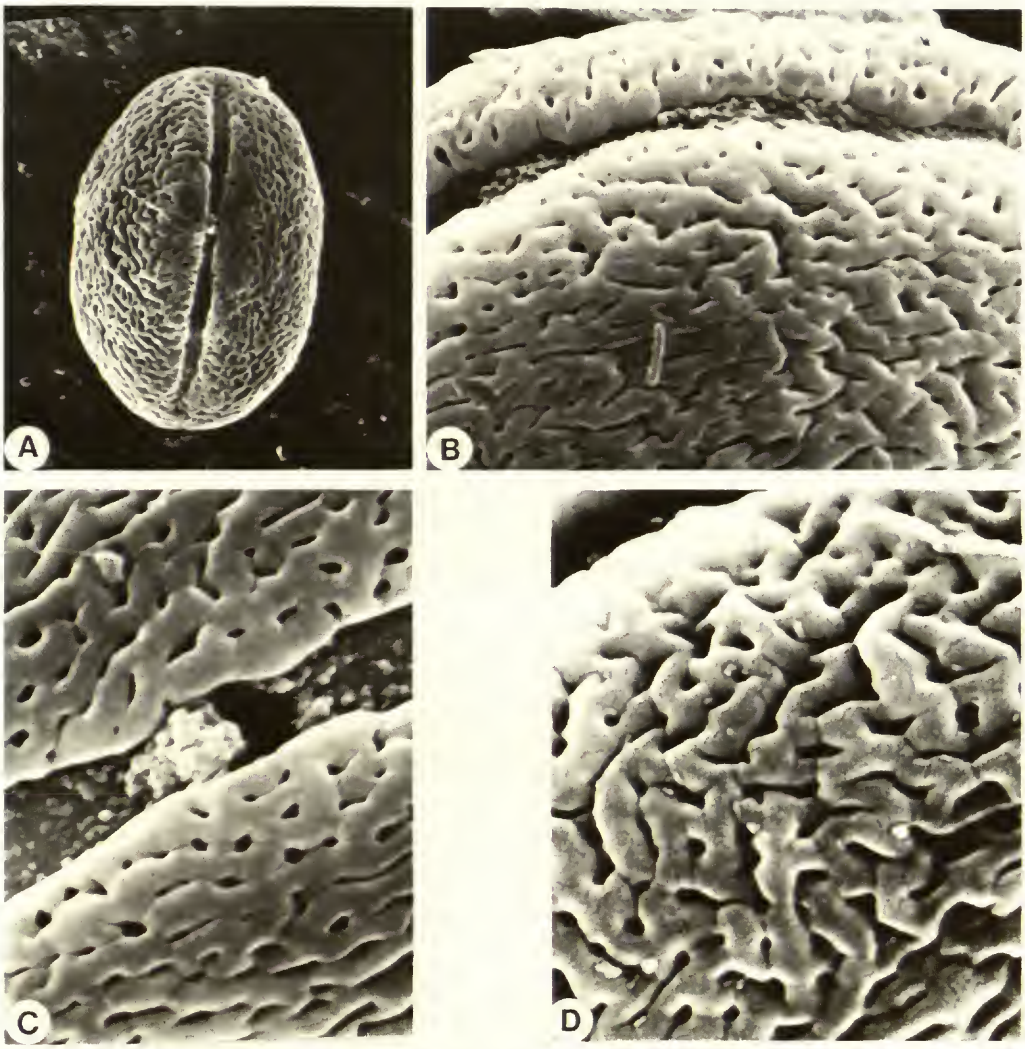


FIGURE 12. Pollen grains of *Bersama* cf. *tysoniana* Oliv. (Melianthaceae).—A. Pollen grain in equatorial view.—B. Mesocolpium and colpus.—C. Detail of aperture.—D. detail of mesocolpal exine. Magnifications: A.×1300; B.×5000; C.×6800; D.×7500. Material *Van der Schijff 5822*, C. (Preparation and photography by J. Praglowski.)

numbers are identical or almost identical for both genera. *Bersama* is reported as $2n = 38$ and *Melianthus* $2n = 36$ & 38 (Federov, 1969).

Phytochemistry. *Bersama* and *Melianthus* are widely used for medicinal purposes, and parts of both genera are toxic (Watt & Breyer-Brandwijk, 1962). In recent years chemical aspects of both genera have received considerable attention. The presence of toxic principles known as bufadienolides in *Melianthus* (Anderson, 1968; Anderson & Koekemoer, 1968, 1969a, 1969b; Koekemoer et al., 1970, 1971, 1974) and *Bersama* (Vanhaelen & Bauduin, 1967; Kupchan et al., 1968, 1971; Kupchan & Ognyanov, 1969; Jethwa & Jackson, 1971; Vanhaelen et al., 1972) strongly supports a relationship between the two genera. The taxonomic value of the bufadienolides as markers of phylogenetic affinity among higher taxa of plants is not clear (after all, they are also present in some toad species!).

A saponin test on leaf material of Melianthaceae was negative (Gibbs, 1974), and Cronquist (1981) considered the family not saponiferous.

However, a simple froth test by Radlkofer (1890) suggested the presence of saponins in the aril of *Bersama*. More recently a saponin was extracted from *B. yangambiensis* Toussaint (Vanhaelen, 1972).

Cyanolipids have been found in the seed oils of Sapindaceae, although not all sapindaceous seeds contain these compounds (for review see Mikolajczak, 1977). Cyanolipids are absent in the seeds of *Melianthus* (Seigler & Kawahara, 1976). A fairly high yield of mangiferin was recorded in *Bersama yangambiensis* (Vanhaelen, 1972). Gibbs (1974) listed Anacardiaceae as the only family of the Sapindales in which this pigment was known to occur at that time. Richardson (1983) reviewed the taxonomic significance of mangiferin and concluded that at all levels the compound appears to be of little taxonomic value.

Fungal or animal parasites. Although members of the parasitic fungus genus *Phyllachora* Nitsthke ex Fickel have been recorded from diverse hosts, particular species of *Phyllachora* are often confined to host species of the same genus. It may therefore be significant that *Phyllachora melianthi* Sacc. has only been found on various species of *Bersama* and *Melianthus major* (Doidge, 1950; Gorter, 1981).

The larvae of the butterfly *Anthene definita definita* Butler (Lycaenidae) utilize a fairly wide range of food plants. However, *Bersama,* Sapindaceae, and Anacardiaceae are the only taxa of the Sapindales recorded (Clark & Dickson, 1971; Pennington, 1978). Most members of the Lycaenidae have their food plants restricted to a single family or even a single genus of plants (Clark & Dickson, 1971). It may therefore be taxonomically significant that another lycaenid butterfly, *Phasis thero thero* L., is recorded from both *Melianthus major* and species of *Rhus* L. (Anacardiaceae), whereas all the other southern African species of *Phasis* are only known to breed on various *Rhus* spp. (Clark & Dickson, 1971; Pennington, 1978). In the family Charaxidae, *Charaxes acuminatis* has been recorded on *Bersama abyssinica* and species of *Allophyllus* L. (Sapindaceae). *Charaxes pollux gazanus* is known to breed on *Bersama abyssinica,* species of *Sorindeia* Thou. (Anacardiaceae), and *Securinega virosa* (Roxb. ex Willd.) Pax & K. Hoffm. (Euphorbiaceae) (Williams, 1969; Pennington, 1978). This regularity in the appearance of Melianthaceae, Sapindaceae, and Anacardiaceae among the food plants of specific butterflies may well reflect taxonomic affinity between these families—particularly in view of their placement in the same order (e.g., Dahlgren, 1983).

Conclusions and relationships. Despite the conspicuous differences between *Bersama* and *Melianthus* (Table 2), evidence from various sources strongly supports a relation between the two genera. These include: multilacunar nodes, similarities in the vascular supply of the leaf, amphivasal medullary bundles, glandular trichomes in some species, presence of styloids, similar chromosome numbers, bufadienolides, comparable ovule and seed development, and shared fungal parasites. *Bersama* and *Melianthus* are nevertheless well defined and appear to have had a long independent history.

With the exclusion of *Greyia,* Melianthaceae are a clearly circumscribed and natural family. Diagnostic features include the presence of styloids, well-developed stipules that are often (not always) intrapetiolar, multilacunar nodes, toxic bufadienolides, an extrastaminal and usually unilateral disc (sometimes annular in *Bersama*), ovules with a multiserial outer integument developing into a multiplicative unlignified testa (epidermal layer of macrosclereids present in *Melianthus*), embryogeny of the Penaea variation of the Asterad type, and the presence of copious endosperm in the seeds.

Melianthaceae are well placed in the order Sapindales and have affinities with Sapindaceae and probably also Anacardiaceae. A possible distant connection with the latter, particularly through *Bersama,* needs further investigation.

Ptaeroxylaceae Sonder

Description. Evergreen to deciduous shrubs or trees, young growth often puberulous. Leaves opposite and paripinnate (*Ptaeroxylon* Eckl. & Zeyh.) or alternate and imparipinnate (*Cedrelopsis* Baill.); leaflets 3–16-jugate, often with the base asymmetric, entire; exstipulate. Inflorescence axillary, multiflorous, contracted thyrses or paniclelike (imperfectly known in *Cedrelopsis*); bracts and bracteoles often caducous. Flowers dioecious (*Ptaeroxylon*) or polygamous (*Cedrelopsis*), actinomorphic, tetramerous (*Ptaeroxylon*) or pentamerous (*Cedrelopsis*). Sepals 4 or 5, with open or imbricate aestivation, free or slightly connate basally, not covering the petals in bud, deciduous. Petals 4 or 5, valvate or imbricate, free, recurved, much longer than the sepals. Sta-

mens 4 or 5, free, alternipetalous, reduced to staminodes in female flowers; filaments glabrous; anthers dorsifixed, versatile, 2-thecate, 4-sporangiate, introrse, longitudinally dehiscent. Pollen grains shed as monads. Disc well developed, intrastaminal, annular or cushionlike in male flowers (*Ptaeroxylon*; *Cedrelopsis*?), fused to the base of the ovary to form a thick "gynophore" in female flowers, bright orange and nectariferous in *Ptaeroxylon*. Ovary superior, inserted on the disc in female flowers, rudimentary and often embedded in the disc in male flowers, with 3–5 (*Cedrelopsis*) or 2 locules (*Ptaeroxylon*), radially symmetric (*Cedrelopsis*) or laterally compressed (*Ptaeroxylon*), glabrous or hairy; ovules 1 (*Ptaeroxylon*) or 2 (*Cedrelopsis*) per locule, ventral hypotropous, campylotropous or subcampylotropous, with axile placentation; styles 2–5, short, connate; stigma conspicuously 2-lobed (*Ptaeroxylon*) or 3- and 5-lobed (*Cedrelopsis*). Fruit a capsule, dehiscing from the central column, this (*Ptaeroxylon*) breaking up into four fibrous strands. Seeds one per locule, flattened with a long terminal wing, exarillate; testa papery, brownish, without endosperm; embryo bent; cotyledons accumbent, fleshy, very oily, chlorophyllous (at least *Ptaeroxylon*).

General information. A small family of woody plants composed of two genera: *Ptaeroxylon* with only *P. obliquum* (Thunb.) Radlk. endemic to eastern and southern Africa, and *Cedrelopsis,* with about seven species endemic to Madagascar.

Specimens of *Ptaeroxylon obliquum* from different areas are often strikingly different in habit and in the size and color of the leaves. Both deciduous and evergreen forms have been recorded. Despite the existence of intermediates connecting some forms (White & Styles, 1966), taxonomic subdivision of the species seems desirable. The timber is extremely durable and very handsome (Von Breitenbach, 1965). Sawdust of dry wood has a peppery smell and provokes violent sneezing, hence the common name "sneezewood" or "nieshout."

Treatment in the literature. Sonder (1860) placed *Ptaeroxylon* in Ptaeroxylaceae, which he doubtfully placed after Sapindaceae. Leroy (1959) added *Cedrelopsis* to Ptaeroxylaceae and gave reasons for maintaining the family distinct from, but related to, Sapindaceae. Subsequently Leroy (1978) suggested that Ptaeroxylaceae may constitute a subfamily of the Simaroubaceae. Takhtajan (1980) recognized Ptaeroxylaceae and related it to Kirkiaceae (usually treated as subfamily Kirkioideae of the Simaroubaceae). *Ptaeroxylon* has also been placed in Sapindaceae (Hooker, 1862). Radlkofer (1890) transferred *Ptaeroxylon* from Sapindaceae to Meliaceae, where it was retained by Harms (1940). Pennington and Styles (1975), however, excluded *Ptaeroxylon* and *Cedrelopsis* from Meliaceae and suggested that they are best treated as a separate family. Ptaeroxylaceae are maintained by White & Styles (1966, 1968a) and Dyer (1975) and also recognized by Thorne (1983) (near Meliaceae) and Dahlgren (1983) (near Rutaceae and Cneoraceae) but not by Cronquist (1981), who included it in Sapindaceae with some hesitation. Airy Shaw (1973) considered Ptaeroxylaceae (and Flindersiaceae) to be somewhat intermediate between Meliaceae and Rutaceae and questioned whether *Kirkia* Oliv. should not be included here. Jenkins (1961), according to Pennington & Styles (1975), suggested a close affinity between Ptaeroxylaceae and Rutaceae through the somewhat anomalous genus *Amyris* P. Br., which also shows some resemblance to Sapindaceae. Hartley (1969) also suggested that there might be significant similarities between Ptaeroxylaceae and the subfamily Flindersioideae (Flindersiaceae of some authors) of the Rutaceae.

Macromorphology. Ptaeroxylaceae have been described as a family of *aromatic* trees and shrubs (e.g., Airy Shaw, 1973; White & Styles, 1966). We were unable to verify this in live plants of *Cedrelopsis,* but at least *P. obliquum* is surely not aromatic (despite the presence of secretory cells in the leaves)—unless these references also pertain to the sawdust (see earlier text). Gross morphology (see, for example, Harms, 1940; White & Styles, 1966; Leroy, 1959) is of a generalized nature and will not be considered in detail.

The nectary in female flowers of both *Cedrelopsis* and *Ptaeroxylon* is rather unusual in that it forms a distinct stalk supporting the ovary (Leroy, 1959). It is bright orange in *Ptaeroxylon,* thereby forming a striking contrast to the yellowish green petals and dark green ovary. The color in *Cedrelopsis* is unknown to us. Leroy (1959) speculated that tetramerous flowers with bicarpellate ovaries and uniovulate locule in *Ptaeroxylon* may have evolved from an ancestor with pentamerous flowers with five carpellate ovaries and biovulate locules as exemplified in *C. grevei* Baill. A possible intermediate stage could

have been similar to the pentamerous flowers with three carpellate ovaries and biovulate loculesas in *C. trivalvis* J.-F. Ler.

Ptaeroxylon obliquum is pollinated mainly by honeybees. The flowers are nectariferous and scented. The winged seeds are distributed by wind.

Anatomy. The presence of secretory cells in the leaves of *Ptaeroxylon* was one of the features that prompted Radlkofer (1890) to transfer the genus from Sapindaceae to Meliaceae—a family characterized by the occurrence of this type of cell. Secretory cells are also present in *Cedrelopsis* (Harms, 1940; Leroy, 1959).

Kribs (1930) considered the wood anatomy of *Ptaeroxylon* to resemble most closely that of the Rutaceae and therefore excluded the genus from Meliaceae. Pennington & Styles (1975) also regarded the wood of *Ptaeroxylon* as definitely not meliaceous and noted similarities with species of both Rutaceae and Sapindaceae. However, on the basis of wood anatomical features, Heimsch (1942) concluded that Rutaceae, Simaroubaceae, Meliaceae, Sapindaceae, Burseraceae, and Anacardiaceae form a natural group. Rutaceae nevertheless seem to be somewhat different owing to their general lack of septate fibers, although they still have much in common with the Simaroubaceae. Septate fibers are also absent in *Ptaeroxylon* (Kromhout, 1975). Wood of *Ptaeroxylon* does not indicate a close link with the Simaroubaceae (wood anatomical data from Webber, 1936). There is some resemblance with subfamily Kirkioideae (with septate fibers and sparse axial parenchyma), but the relationship is not very close. However, there are so many exceptions and inconsistencies in wood features that care must be taken not to overemphasize its systematic value in Ptaeroxylaceae and any of the other aforementioned families.

Pollen morphology. Erdtman (1952) noted the reticulate sexine of *Ptaeroxylon* pollen grains, and Lobreau-Callen et al. (1975) compare pollen grains of *Cedrelopsis* with the *Turraea*-type (Meliaceae), which is also (at least in some species) characterized by a reticulate sculpturing of the sexine. Pennington & Styles (1975) confirmed that the pollen grains of *Ptaeroxylon* and *Cedrelopsis* are very similar, but confidently stated that the grains differ in several important respects from those of all known Meliaceae. They seem to resemble the grains of Rutaceae, although not very closely.

Embryology and seed. The ovule structure of *Ptaeroxylon obliquum* was briefly discussed by Mauritzon (1936) and compared with previous observations by Radlkofer (1890). It is bitegmic, crassinucellate, campylotropous, and hypotropous. Mauritzon (1936) considered the hypotropous state to strongly favor excluding *Ptaeroxylon* from Meliaceae (a position favored by Radlkofer), in which the ovules are usually epitropous. Ovules of *Ptaeroxylon* are remarkable in being conspicuously winged (mainly an outgrowth of the chalazal part). Mauritzon (1936) nevertheless considered the marked bending of the nucellus and the straight and almost direct (ovules sessile) vascular supply in both *Ptaeroxylon* and *Sapindus* L. to be indicative of an affinity between the two taxa. On the basis of ovule structure, Mauritzon strongly advocated the placement of *Ptaeroxylon* in Sapindaceae. A position in Sapindaceae is also favored by the curved radicle in *Ptaeroxylon*.

The testa of *Ptaeroxylon* has a papery and somewhat spongy texture. This is obviously an adaptation to its anemochoric dispersal. Variable numbers of cells filled with a pinkish orange substance are present in the deeper layers of the testa, mainly in the embryo containing part of the winged seed. Courchet (1906), according to Harms (1940), referred to these as oil cells.

Chromosome number. Apparently still unknown.

Phytochemistry. Various parts of *Ptaeroxylon* and *Cedrelopsis* are used for medicinal purposes (Harms, 1940; Watt & Breyer-Brandwijk, 1962). It is therefore not surprising that both genera have been the subject of numerous chemical studies (though rarely to determine biological activity).

Ptaeroxylon obliquum wood contains a remarkable range of chromones and some unusual coumarins (Dean et al., 1967; McCabe et al., 1967; Eschiet & Taylor, 1968). These are closely matched by the heartwood constituents of *Cedrelopsis grevei* (Eschiet & Taylor, 1968; Dean & Robinson, 1971). Phytochemistry fully supports the view that *Ptaeroxylon* and *Cedrelopsis* are closely related.

Chemical evidence has proved to be extremely useful for the elucidation of affinities between the families of the Rutales (Gershenzon & Mabry, 1983; Waterman & Grundon, 1983). Limonoids (for reviews, see Dreyer, 1968, 1983; Connolly, 1983; Taylor, 1983; Das et al., 1984)

are found only in Meliaceae, Rutaceae, Cneoraceae, and *Harrisonia abyssinica* Oliv. (Straka et al., 1976; Taylor, 1981), either Simaroubaceae or perhaps congeneric with *Spathelia* L. (Rutaceae) (Dreyer, 1983; Taylor, 1983). A group of related compounds, the quassinoides (simaroubolides), are confined to the Simaroubaceae (Dreyer, 1968; Waterman, 1975; Polonsky, 1983). Neither limonoids nor quassinoides are present in Ptaeroxylaceae (Waterman & Khalid, 1981).

Coumarins and chromones are produced by Ptaeroxylaceae, Cneoraceae, and Rutaceae but rarely by Meliaceae and Simaroubaceae (Waterman, 1975; Waterman & Khalid, 1981; Gray, 1983). Waterman (1975) pointed out that the coumarins cedrelopsin and brayelin are present in both *Cedrelopsis* and *Flindersia* (Flindersioideae, Rutaceae). He also noted similarities between the coumarins (particularly the substituted ethylene-dioxy group) of *Ptaeroxylon* and *Haplophyllum* A. Juss. corr. Reichb. (Rutaceae), as well as the presence of the chromone *allo*-ptaeroxylin, in both *Ptaeroxylon* and *Spathelia* (Spathelioideae, Rutaceae). Very similar coumarins have been isolated from Ptaeroxylaceae and Cneoraceae (Gray, 1983). Ptaeroxylaceae and species of *Spathelia* (Rutaceae) also share some chromones with members of Cneoraceae (Waterman, 1975; Waterman & Khalid, 1981; Gray, 1983). Waterman & Khalid (1981) suggested that from a biochemical point of view Ptaeroxylaceae (southern Africa and Madagascar), Cneoraceae (Canary Islands, Mediterranean, Cuba) and the Spathelioideae (West Indies) appear to be the disjunct remnants of a former, more widespread group of chemically similar taxa. Despite the co-occurrence of coumarins, Ptaeroxylaceae and Flindersioideae do not appear otherwise to be biochemically very closely related (Waterman & Khalid, 1981; Waterman, 1983).

Alkaloids of various types are present in Rutaceae and only rarely in Simaroubaceae (mainly the Simarouboideae) and Meliaceae (one species). There are no reports of alkaloids in Cneoraceae or Ptaeroxylaceae (Waterman & Khalid, 1981; Gershenzon & Mabry, 1983; Mester, 1983).

Fungal or animal parasites. A connection between Ptaeroxylaceae and Rutaceae is supported by the feeding habits of the butterfly, *Papilio demodocus* Esper. (family Papilionidae, subgenus *Papilio* L.). Members of this subgenus breed almost exclusively on members of the Rutaceae, whereas subgenus *Graphium* is confined to Annonaceae. *Papilio demodocus* (*Princeps demodocus* (Esper) of some authors) breeds predominantly on Rutaceae. However, the presence of larvae were also recorded on *Pseudospondias* Engl. (Anacardiaceae), *Hippobromus pauciflorus* (L. f.) Radlk. (Sapindaceae), *Ptaeroxylon obliquum*, and members of *Apiaceae* (Van Son, 1949; Ehrlich & Raven, 1964; Williams, 1969; Pennington, 1978). Larvae (final instar) on Apiaceae show a variegated pattern that is quite different from the plainer greenish coloration found on Rutaceae and Ptaeroxylaceae (Pennington, 1978). The occurrence on Apiaceae may seem anomalous, but, as Thorne (1979) pointed out, phytophagous insects should rather be considered good chemists and not necessarily good taxonomists. In this connection McCabe et al. (1967) noted that, similar to Ptaeroxylaceae, both chromones and coumarins co-occur in members of the Apiaceae. Pachler & Roux (1967) reported peucenin (a chromone) in wood of *P. obliquum*. This compound is also known from *Peucedanum ostruthium* Link. (Apiaceae). Peucenin was subsequently also recorded in the heartwood of *Cedrelopsis grevei* (Dean & Robinson, 1971). Chemical evidence clearly favors the hypothesis that the Araliales (Apiaceae and Araliaceae) and perhaps also Asterales may have evolved from Rutalean stock (Hegnauer, 1971, 1983). There are chemical ties linking Apiaceae mainly with Simaroubaceae, Rutaceae, and Ptaeroxylaceae.

The parasitic fungus *Meliola ptaeroxyli* Doidge is only known from *Ptaeroxylon obliquum*. Other species of *Meliola* Fr. occur on many diverse genera (including Meliaceae and Rutaceae) (Doidge, 1950; Gorter, 1981).

Conclusions and relationships. Possible affinities between Ptaeroxylaceae and Sapindales s. str. (notably Sapindaceae) suggested by ovule structure and, to a lesser degree, vegetative anatomy are almost overwhelmingly contradicted by the available phytochemical evidence. The distinctness of the Ptaeroxylaceae and its placement in the Rutales are fully supported by phytochemical evidence. Its affinities are with Rutaceae rather than Meliaceae, although both have probably evolved from proto-rutaceous stock (Waterman & Khalid, 1981; Gershenzon & Mabry, 1983).

We follow Waterman (1983) in considering Ptaeroxylaceae a natural family related to Rutaceae (especially through the subfamily Spathelioideae), Cneoraceae, and perhaps also Sima-

roubaceae (through *Harrisonia*). A detailed comparative morphological, anatomical, and embryological study of these taxa may be a fruitful area for future research. The genus *Cedrelopsis* is still comparatively little known.

Aitoniaceae Harvey

Description. Evergreen to drought-deciduous shrubs or small trees, (0.5)1–2(4) m high, much branched with long shoots and brachyblasts; branchlets puberulous to pubescent. Leaves simple, alternate or usually fascicled on cushionlike brachyblasts; lamina linear to linear-oblanceolate, entire, coriaceous, puberulent to glabrous, usually with one to several minute and irregularly spaced extrafloral nectaries particularly near the midrib on the lower surface, tapering at the base into a short petiole; lateral veins present but obscure; stipules wanting. Flowers solitary or rarely in shortly peduncled (up to 4 mm long) 3-flowered dichasia, axillary, hermaphrodite, slightly zygomorphic, 4-merous, hypogynous, more or less urceolate at anthesis, becoming campanulate with age, distinctly protogynous, unscented, nectariferous; pedicels (6)8–15(20) mm long, held roughly perpendicular to the shoot axis with the flowers presented more or less horizontally, slightly bent, often approaching an open S-shape, gradually thickened distally, subtended ca. 1 mm above the base by two minute opposite bracteoles, puberulent. Calyx deeply 4-lobed with open aestivation; sepals ovate, often tinged with pink, puberulent, minutely ciliate. Petals 4, free, sessile, imbricate, much longer than the calyx, relatively thick, oblong-elliptic, concave, apices reflexed, coherent at first, spreading with age, greenish pink, coral pink or purplish (the color usually most intense on surfaces directly exposed to the sun), puberulent, particularly on the dorsal surface. Stamens 8, exserted, coherent, ascending in newly opened flowers; filaments green, at anthesis progressively shorter from the dorsal to the ventral position, flattened dorsiventrally, particularly toward the base, united in about the lower third in a cylindrical tube, this slightly shorter ventrally, filled with nectar at anthesis; anthers at anthesis usually directed ventrally owing to the distal twisting of some of the filaments, variously directed in older flowers, bright orange (pollen grains visible through the anther wall), glabrous, dorsifixed, versatile, 2-thecate, 4-sporangiate, erect in bud, introrse, longitudinally dehiscent. Pollen grains shed as monads, bright orange, and clumping together when fresh. Disc intrastaminal, patelliform, fleshy but rather inconspicuous and partly supporting the ovary, margin slightly crenate. Ovary superior, sessile, truncate, densely pubescent, 4-lobed, 4-locular; ovules two per locule, collateral on a subapical axile placenta, ventral epitropous, campylotropous, subsessile with the micropyle appressed to a conspicuous placental obturator; style terete, ascending, extending beyond the stamens; stigma simple and indistinct. Fruit an inflated chartaceous capsule, 4-lobed, acutely 4-angled, 4-locular, greenish white or pink to reddish, up to 40 mm diam., remaining on the plants for many weeks, being dispersed when the seeds ripen, opening as a result of weathering. Seeds 1–4(8) per fruit, brownish black, reniform, exarillate; testa hard with the warty surface minutely papillate; embryo following seed curvature, chlorophyllous; cotyledons more or less linear, flat, collateral; radicle superior, exserted; endosperm present as a thin layer lining the seed coat.

General information. *Nymania capensis* (Thunb.) Lindl. (= *Aitonia capensis* Thunb.) is the only species—perhaps with two varieties. It is a rigid, much-branched shrub or small tree confined to arid parts of the Cape Province and the southern parts of Namibia. Crushed leaves may emit an unpleasant odor, particularly in plants from the northwestern Cape and Namibia (var. *microphylla* Schinz). The shoots and leaves are extremely bitter. The inflated pinkish capsules have a silvery sheen and are particularly attractive. They give rise to two of the common names for the species, "Klapperbos" and "Chinese lanterns." Despite its considerable horticultural potential, the species seldom survives for long outside its semidesert environment.

Treatment in the literature. The taxonomic history of *Nymania* has been outlined by Pennington & Styles (1975) and will not be repeated here in detail. It has been variously referred to Meliaceae, Sapindaceae, Rutaceae, Zygophyllaceae, Malvaceae, and even to its own family, Aitoniaceae (e.g., Harvey, 1860; Airy Shaw, 1973; Dyer, 1975). Airy Shaw (1973), like many earlier authors, suggested that Aitoniaceae are most probably closest to Sapindaceae. However, Radlkofer (1890) strongly disagreed with its inclusion in Sapindaceae and related it to Meliaceae. This view was subsequently followed by most authors.

In their generic monograph of Meliaceae, Pennington & Styles (1975) maintained that *Nymania* clearly belongs to tribe *Turraeeae,* subfamily Melioideae. A detailed examination of its morphology, wood anatomy, and pollen led them to conclude that it is closely related to the Malagasy genus *Calodecaryia* J. F. Leroy, which seems to link it to *Turraea* L.

Although referred to Meliaceae already by De Jussieu (1789), *Nymania* displays a number of characters rare or absent in other members of the family. These include the bell-shaped and slightly zygomorphic flowers with curved filaments and style, colorful mature petals that are not conspicuously reflexed, absence of an expanded style head, filaments that are only fused at the base (up to one-third their length in some flowers), dorsifixed versatile anthers with the connective not produced to form a long terminal appendage, inflated capsules (distinctly sapindalean in appearance), presence of some pore clusters, and the lack of gum in the wood, fibers nonseptate and isobilateral, and amphistomatic leaves. Whether *Nymania* is indeed a member of the Meliaceae will again be critically explored in the present account. Should this be the case, possible explanations for its somewhat anomalous features will be attempted. See White (1986) and White & Styles (1986b) for accounts published since this paper went to press.

Macromorphology. Goldblatt (1976) noted that seedlings of *Nymania* grown for cytological study produced deeply trilobed leaves dotted with what he called chalk glands. This should be considered the exception rather than the rule. Our own observations on seedlings revealed only simple, entire leaves similar to those of the mature plant. Neither is the phenomenon mentioned by Pennington & Styles (1975), who also described the seedlings of the species. The chalk glands could be equivalent to what we call multicellular glandular hairs, or perhaps refer to the whitish dots caused by the substomatal chambers (see further on in text).

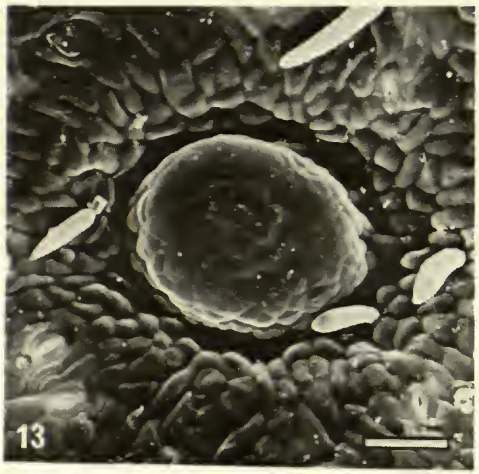
At least some of the cushionlike brachyblasts retain their potential to elongate and occasionally resume apical growth to become long shoots.

Extrafloral nectaries (epidermal nectaries in the sense of Wilkinson, 1979) were noticed in all the specimens examined. These depressed, circular or elliptic areas occur mainly on the lower lamina surface (Fig. 13). They vary in number and position from leaf to leaf and tend to be confined toward the proximal end of the lamina, usually on or near the midrib. They occasionally seem to be absent from some leaves. Meliaceae are not listed by Metcalfe & Chalk (1979) or Elias (1983) among the families in which extrafloral nectaries have been observed. Extrafloral nectaries were also recently discovered in other Meliaceae (Lersten & Rugenstein, 1982; N. R. Lersten, pers. comm.).

Another feature hitherto undetected in *Nymania* is the occasional presence of three-flowered dichasia in some plants. In many genera of the Meliaceae the ultimate ramifications of the inflorescence are cymose (Pennington & Styles, 1975). It is therefore possible that the usually single flowers of *Nymania* represent a reduction from a panicle (perhaps terminating in cymules), with the dichasium reflecting one of the intermediate stages of evolution. The presence of minute bracteoles on the pedicels supports this hypothesis.

The flowers of *Nymania* are bird pollinated (Vogel, 1954). There is evidence that sunbirds (family Nectariniidae) are the primary pollen vectors. The flowers clearly display the syndrome for ornithophily (Faegri & Van der Pijl, 1979). They approach the so-called gullet type with oblique profile. Notable adaptations of the flowers include the pink or red color of the petals; loose overlapping petals that easily spread apart; abundant production of nectar; lack of odor; attractive dark green filaments with bright orange versatile anthers that project well beyond the petals; filaments that are curved upward, the lower ones progressively shorter to allow easy access to the nectar from below; a style that projects well beyond the filaments; and a staminal tube with the filaments only fused toward the base to allow easy access to the nectar and prevent possible damage to be caused by a probing bill. The flowers often extend outward from the stems on long pedicels, but sunbirds have no difficulty in taking nectar by hovering in front of a flower (Skead, 1967).

Observations on *Nymania* in the Karoo Botanical Garden, Worcester (J. Forrester, pers. comm.) showed that flowering plants attract large numbers of lesser double-collared sunbirds. The birds prefer the partly opened (urceolate) flowers and do not approach the more fully opened campanulate ones. In the former stage the staminal tube is completely filled with nectar, the anthers are often still closed, and the stigma is well exserted and apparently receptive. The campanulate shape is attained soon after the anthers have dehisced. No nectar is secreted after anthesis.



FIGURES 13, 14. Scanning electron micrographs of leaf surfaces in *Nymania capensis* (Thunb.) Lindl.—13. Abaxial surface showing a presumably extrafloral nectary.—14. Adaxial surface showing a multicellular glandular trichome. Scale line = 50 μm.

Bees were active particularly on the more open (and now nectarless) flowers. Several ants were also noted, some moving to the partially opened flowers where they buried their forequarters into the flowers amongst the stamens, obviously trying to reach the nectar.

The attractive inflated capsules of *Nymania* are adapted for wind distribution (Marloth, 1896). They remain on the plant for many months but are eventually shed and effectively dispersed by the wind.

Anatomy. Anatomical observations confirm the presence of secretory cells in the mesophyll of the lamina (already reported by Radlkofer, 1890). However, they are not very distinct and do not show up as transparent dots on the leaves. Secretory cells are common in both Meliaceae and Sapindaceae. In support of their inclusion of *Nymania* in Meliaceae, Pennington & Styles (1975) stated that the continuous ring of sclerenchymatous tissue present in the bark of the twigs of Sapindaceae is absent from *Nymania*, as it is from all other Meliaceae. This is obviously an erroneous interpretation of the original statement by Radlkofer (1890), who referred to a *composite* sclerenchymatous cylinder in the cortex of the twigs (viz., both fibers and sclereids). An almost continuous or continuous ring of extraxylary *fibers* is present in *Nymania*, as in many other Meliaceae.

Noteworthy anatomical features of *Nymania* apparently not previously recorded are the presence of multicellular grandular hairs (in addition to simple unicellular ones and distributed mainly on the upper lamina surface) (Fig. 14) and amphistomatic leaves with a tendency toward an isobilateral anatomical structure. Metcalfe & Chalk (1950) recorded only hypostomatic and dorsiventral leaves in Meliaceae. Minute whitish dots visible on both leaf surfaces are caused by conspicuous substomatal chambers. These (or the glandular hairs) could well be the so-called "chalk glands" mentioned by Goldblatt (1976). The stomata are anomocytic and the surrounding epidermal cells slightly overarch the guard cells from below. This pattern was also described in other Meliaceae (Pandey, 1969) and might be characteristic for the family.

Pollen morphology. The pollen morphology of *Nymania* is described by Pennington & Styles (1975). They noted that although the pollen grains (with scabrous or rugulose exine) look different from typical Meliaceae pollen, they are fairly similar to those of *Humbertioturraea* J. F. Leroy and some species of *Turraea.*

Embryology and seed. The embryology of *Nymania* has not yet been studied in detail (Mauritzon, 1936). Superficial observations have shown that the ovules are subsessile, campylotropous, ventral epitropous, bitegmic, and crassinucellar. Each locule contains two collateral ovules. The mycropylar region is in close contact with an apical placental obturator consisting of

a spongy tissue (placental hairs?). An obturator is present in many members of the Meliaceae (Nair, 1970) and, together with the other aforementioned features, strongly supports the inclusion of *Nymania* in this family. Although the seeds of *Nymania* have sometimes been described as exendospermous (e.g., Airy Shaw, 1973), the embryo is indeed embedded in a thin layer of endosperm. This confirms other reports that the seeds are endospermous (e.g., Harms, 1940; Pennington & Styles, 1975). In Meliaceae endosperm is present particularly in the *Turraeeae* (Melioideae) (Pennington & Styles, 1975).

No aril or sarcotesta is present in the seeds of *Nymania*. The seeds are reniform and develop from a campylotropous ovule. Bending of the nucellus during ovule and seed ontogeny is accompanied by the inclusion of parenchymatous tissue (mainly integument and funicular) beneath the ventral face of the nucellus. This is a common phenomenon in many curved seeds that develop from campylotropous or especially amphitropous ovules. What Pennington & Styles (1975) considered a sarcotesta in *Nymania* is probably this hump of tissue. Bocquet (1959) and Bocquet & Bersier (1960) called it the basal body ("corps basal"), while others refer to it as the chalazal packet (e.g., B. Singh, 1964; Mathur & Gulati, 1980). It is not synonymous with the hypostase as suggested by Foster & Gifford (1974). Neither does it conform to a sarcotesta in the usual meaning of the term (cf. Corner, 1976).

Chromosome number. Chromosome counts for *Nymania* vary. Styles & Vosa (1971) recorded $2n = 40$ and Goldblatt (1976), $2n = 48$. These fairly high counts seem to be consistent with the pattern in Meliaceae, a family also characterized by a high frequency of polyploidy (Federov, 1969; Styles & Vosa, 1971; Datta & Samanta, 1977).

Phytochemistry. Phytochemical evidence strongly supports the placement of *Nymania* in subfamily Melioideae of the Meliaceae. MacLachlen & Taylor (1982) found *N. capensis* to be a rich source of limonoids related to the more complex *Trichilia* type. The limonoid bitter principles are almost entirely confined to the Meliaceae, Rutaceae, and Cneoraceae (Dreyer, 1968; Straka et al., 1976; Taylor, 1981; Connolly, 1983; Taylor, 1983; Das et al., 1984). The chemistry of the tribe Turraeeae is poorly known, but *Turraea floribunda* Hochst. also contains limonoids. On the other hand, *Naregamia alata* Wight & Arn. has been investigated but not found to contain limonoids or protolimonoids (Taylor, 1981). In contrast to the leaves of *Nymania capensis*, leaves of *Turraea obtusifolia* Hochst. do not taste bitter. This could indicate the absence of limonoids. Whereas limonoids apparently occur in all species of genera of Rutaceae, this may not always be the case in Meliaceae (Dreyer, 1968).

Conclusions and relationships. Available evidence convincingly supports the placement of *Nymania* in the Meliaceae. The following suggestions are offered to account for the unique combination of features in *Nymania*. *Nymania capensis* is most probably the only member of the Meliaceae confined to semidesert and desert conditions. The linear and rather sclerophyllous leaves are obviously an adaptation to its arid environment. The flowers of *Nymania* are clearly adapted for bird pollination. Modifications of pollen structure and sculpture associated with pollination by birds have been found, for example, in Papilionoideae (Ferguson & Skvarla, 1982). The aberrant exine sculpture in *Nymania* may well be linked to this pollination mechanism. Flowers pollinated by relatively specialized pollen vectors such as birds are less commonly dioecious than others (Willson, 1983), and while many other members of the Meliaceae are functionally dioecious (Styles, 1972; Pennington & Styles, 1975), *Nymania* is not. Whether the extrafloral nectaries in *Nymania* are a device to attract insect guardians (e.g., biting ants) against nectar thieves deserves further study. The many ants noticed on the plants suggest this possibility. The inflated fruits that have often been advanced as evidence for a link with Sapindaceae are clearly a specialized adaptation for wind distribution.

Nymania capensis seems to be the only species in Meliaceae with a combination of xerophytic habit, ornithophilous flowers, and anemochorous fruits. It is a striking example of a species in which adaptation to an unusual (for Meliaceae) combination of environmental factors renders it so different from typical Meliaceae that it has been referred to other families or even a family of its own.

In conclusion, we cite an interesting example of convergent evolution in three unrelated genera—*Nymania, Melianthus* L. (Melianthaceae), and *Sutherlandia* R. Br. ex Ait. f. (Fabaceae)—which often share the same habitat (some species of the latter two genera also occur in regions with relatively high rainfall). Bird pollination was recorded in both *Melianthus* and *Sutherlandia*

FIGURE 15. *Roridula dentata* L. (A–G) and *R. gorgonias* Planch. (H–O) (Roridulaceae).—A, H. Floriferous branches.—B, J. Parts of leaves, showing differences in distribution of hairs.—C, K. Flowers.—D, L. Sepals (left) and flowers sectioned longitudinally.—E, M. Stamens; M also showing the pistil.—F, N. Young fruits.—G, O. Seeds. Material: A–E. *Dahlgren & Strid 3183* (LD); F, G. *Grant 3476* (C); H, N, O. *Esterhuysen 26959* (LD); K–M. Alcohol-fixed material collected by P. Goldblatt at Hermanus.—Del. B. Johnsen.

(Vogel, 1954; Skead, 1967; Arroyo, 1981). Flower color is red or brown in the former genus and bright scarlet in the latter. The fruits of *Melianthus* are inflated papery capsules superficially very similar to those of *Nymania. Sutherlandia* produces inflated papery pods. As in *Nymania,* the fruits of the other two genera are distributed by wind (Marloth, 1896). Also, species of *Nymania* and *Melianthus* are unpleasantly scented when bruised.

Roridulaceae Engler & Gilg

Description. Shrubs sparsely branched, to 2 m, with spirally set leaves clustered toward the branch ends of adult shrubs (see Fig. 15). Leaves flat, dorsiventral, linear, sessile, exstipulate, yellow-green, to 60 mm or rarely 100 mm long, entire or with linear lateral lobes, with brochidodromous venation and, in *Roridula dentata* L., with side veins supplying the lobes. Leaves and young stems with short to long glandular (tentacular) hairs and unicellular bristle hairs (see anatomy). Secretion of tentacular hairs sticky, resinous, without proteolytic enzymes. Inflorescence a few-flowered panicle ("raceme with a terminal flower"), pedunculate, the flowers in the axils of linear bracts. Flowers long- or rather short-pedicellate, the lateral with two lanceolate or linear prophylls; bisexual, actinomorphic, hypogynous, 5-merous in calyx, corolla, and androecium, 3-merous in the gynoecium. Sepals distinct, imbricate, green, lanceolate, glandular-hairy. Petals distinct, imbricate, sessile, broadly ovate to obovate, pointed or rounded, entire, glabrous, purple or crimson to nearly white. Stamens opposite the sepals; filaments distinct, narrow; anthers elongate, tetrasporangiate, introrse, incurved in bud, subtended by a basal swelling containing a nectariferous cavity, irritable, swinging upward when touched at anthesis to become erect; pollen sacs dehiscing by apical slits or pores. Pollen grains dispersed as monads. Pistil syncarpous, trilocular, style simple, terminal, either tapering and with a small, capitate stigma (*R. dentata*) or expanding terminally, apically obconical, with a larger stigma (*R. gorgonias* Planch.); ovules either one per locule (*R. dentata*) or 2–4 (*R. gorgonias*), centrally inserted, anatropous. Fruit a 3-valvular loculicidal capsule; seeds either one per locule, large, narrowly ellipsoidal, smoothly reticulate (*R. dentata*; Fig. 15G) or two per locule, warty to honeycombed (*R. gorgonias*; Fig. 15O), without embryo endosperm; small.

General information. Roridulaceae comprise the single genus *Roridula* Burm. fil. ex. L., with two species, *R. dentata* and *R. gorgonias.* The two species differ considerably, especially in pollen and seed morphology, and *R. gorgonias* may be generically distinct (P. Raven, pers. comm.). The family is endemic to the Cape Province, with *R. dentata* distributed in the mountains from the Tulbagh district through the Koue Bokkeveld (Ceres district) to the Cedarberg mountains, and *R. gorgonias* in the southern mountainous regions mainly between Gordons Bay and Hermanus northwards (inland) to the Genadendal region, principally in the Caledon district. Both species grow in sandy habitats, on substrates weathered from sandstone of the Table Mountain Group. The taller *R. dentata* grows on moderately moist slopes, the slightly shorter *R. gorgonias* mainly along streams with constant water supply.

Treatment in the literature. Due to its sticky, tentacular hairs reminiscent of the glands in Droseraceae and in the Australian unigeneric Byblidaceae, *Roridula* has generally been associated with both or either of these groups in previous classifications from Bentham & Hooker (1862, 1967) to the present day. *Roridula* was thus included in Droseraceae by Darwin (1875), Eichler (1875), Engler & Prantl (1894), Solereder (1908), and Wettstein (1911). It was excluded from Droseraceae by Diels (1906) and transferred to Ochnaceae by Engler (1907). Metcalfe & Chalk (1950), Hutchinson (1959), and Cronquist (1981) placed *Roridula* and *Byblis* Salisb. in one family separate from Droseraceae.

Marloth (1903, 1910, 1925) established early that *Roridula* is not insectivorous (in the sense that proteolytic enzymes are not produced) as is the case with Droseraceae and Byblidaceae; and he referred *Roridula* to a separate family, Roridulaceae.

In an embryological study, Vani-Hardev (1972) demonstrated profound differences between *Roridula* and *Byblis,* and between both of these genera and the Droseraceae, and supported a treatment in three different families. In spite of clarifying the embryology of *Roridula,* he did not draw any conclusions as to relationships between Roridulaceae and other families.

In most treatments, the above families with glandular hairs have been placed in Rosales sensu lato or Saxifragales, but sometimes (as by Hutchinson, 1959) in a separate Pittosporales.

Schulze-Menz (in Melchior, 1964) placed Roridulaceae and Byblidaceae near Pittosporaceae in Rosales suborder Saxifragineae. Takhtajan (1980) also associated Roridulaceae with the same two families in the order Saxifragales. Cronquist (1981) retains both *Roridula* and *Byblis* in his Byblidaceae, which he associates with Pittosporaceae and Hydrangeaceae in his widely circumscribed order Rosales. Dahlgren (1980a, 1983) placed Roridulaceae, with *Roridula* only, in Ericales of his Corniflorae on the basis of floral morphology, embryology, and iridoid contents. Thorne (1968, 1976, 1981, 1983) associated Roridulaceae with Bruniaceae, Grubbiaceae, Geissolomataceae, and Myrothamnaceae, in suborder Bruniineae of the Pittosporales, for which he cited wood anatomical support (Carlquist, 1976b).

Macromorphology. A few complementary notes will be given here on morphology and biology. *Roridula* has a taproot, described as well developed by Bruce (1907). It obviously lacks endotrophic mycorrhiza as is present in members of Ericales.

The inflorescence is determinate, i.e., it is terminated by a flower. Thus it is more related to a panicle than to a true (indeterminate) raceme.

The stamens have an unusual construction adapted to the pollination mechanism (Marloth, 1925). The anthers (as in many Ericales) dehisce by a short apical slit or pore. The hemipteran of the genus *Pameridia* (Miridae, Hemiptera) visits both *Roridula* species, attracted by the nectar produced in the anther swellings. When these are pierced the anthers swing upward, becoming erect and spreading pollen on the insects. Marloth (1925) observed that, unlike other insects, this hemipteran could run over the leaves unhindered by the sticky glands. The many details associated with the structures of the plant and insect indicate an intimate adaptive evolution. (There is also a crab spider, of the genus *Synema,* that is capable of living on the leaves of *R. dentata,* feeding on captured insects, without being stuck on the viscid glands.)

The differences between the two species of *Roridula* concern total size, leaf shape, density and distribution of hairs, pedicel length, shape of anthers, seed, shape of style, lobation of ovary, number of ovules, shape and surface sculpture, and especially pollen grain characters. The basic morphology, including such complex features as gland construction and anther morphology, is similar, however; and a close relationship between the two species is undisputable. The question as to whether the two species should be treated as congeneric is not addressed here.

Anatomy. The wood of *Roridula* has indistinct growth rings or none at all (Carlquist, 1976b). The vessels are long and have oblique perforation plates with scalariform perforations and bordered bars. *Roridula gorgonias* has 37–83 (average ca. 50) bars per plate, *R. dentata* 3–23 (average ca. 10) bars per plate in the stem vessels, a considerable difference. This is at least partly associated with differences in water availability for the two species (greater for *R. gorgonias*) (Carlquist, 1976b). Vessel rays are mostly uniseriate (rarely biseriate), and the ray cells are exclusively upright. Gummy deposits are present in some ray cells, while crystals are lacking in the wood. On the basis of wood anatomy, Carlquist considered Roridulaceae to be comparable with woody Saxifragaceae, Cunoniaceae, Hamamelidaceae, Bruniaceae, Grubbiaceae, and Daphniphyllaceae but not particularly closely related to Byblidaceae and not closely at all to Droseraceae.

The leaf venation in *Roridula gorgonias* is clearly brochidodromous (Bruce, 1907, fig. 6) and similar in *R. dentata,* in which the marginal veins produce laterals to the lobes, which makes the pattern different. The leaf cuticles are thin. Stomata are anomocytic and present on both sides of the leaves. They are not notably sunken and are oriented parallel to the leaf axis.

The tentacular hairs are (usually) not vascularized as they are in Droseraceae. They vary from short and rather few-celled (with a uniseriate stalk and ca. six flattened cells making up the head) to long and multicellular, with a long stalk five cells across (in transection) and a head with a central column three cells across, on which the glandular cells are situated. These are basally attached to the gland head column but are not laterally attached to each other. They contain resinous material and, according to Bruce (1907), their ability to dissolve albumen was none or little.

The tentacular hairs are different from those in both Droseraceae and Byblidaceae, and the glands in the three families undoubtedly have evolved by convergence. Although the glands in *Roridula* are unable to dissolve captured flies and utilize their nitrogen-rich tissues, the withered and shed leaves (with their insects) may contrib-

ute to improving the soil (Carlquist, 1976b). The glands are generally considered to protect the flowers from unwelcome visits by insects or snails, but their function may be simply to protect the plant from being eaten by herbivores. The bristle hairs are unicellular processes from short epidermal hairs. Bristle hairs and tentacular hairs differ in density and concentration between the two species, the latter generally more densely set on *R. dentata* than *R. gorgonias*. The largest tentacular hairs in both species are situated on the leaf margins, in *R. dentata* on the lateral lobes.

Oxalate crystal druses occur in epidermal cells, especially along the main veins (Bruce, 1907).

Between the one-layered epidermis on the lower side and that on the upper side there are several layers of more or less loose chlorenchyma, this much denser in *Roridula gorgonias* than in *R. dentata*. In the latter the chlorenchyma has a reticulate organization with cells meeting only at their ends. On the abaxial surface the midvein is subtended by a tissue of large empty cells, either 3-layered with a middle row of conspicuously large cells (*R. gorgonias*), or 4–6-layered with less regular rows and with subequally large cells (*R. dentata*) (Bruce, 1907).

Pollen morphology. The pollen grains of the two species of *Roridula* are very different. Those of *R. dentata* (Fig. 16A–D) are isopolar, radially symmetrical, presumably 3-colporate (3-colporoidate, according to Erdtman, 1952), prolate-spheroidal, with the polar axis 36.5 μm and equatorial diameter ca. 36 μm. The exine sculpture is characterized by a spinuliferous tectum with distinct perforations, supported by infratectal bacula. The ora are indistinct, and the colpus membrane exhibits granular ornamentation at the edges and is warty in the center, thus resembling the nonapertural exine (see also Van Zinderen-Bakker, 1956).

In contrast, *Roridula gorgonias* (Fig. 16E–I) has apolar, asymmetrical, spheroidal pollen grains ca. 50 μm in diameter, without distinctly developed apertures. The exine of the apertural regions has irregular circular fissures. A coherent tectum is lacking. The exine structure is insular, with polygonal to rounded elements supported by bacula and separated from each other by narrow spaces, and decreasing somewhat in size towards the apertural fissures. The pollen grains of *R. dentata* are the basic type and represent a transitional 3-colpate/3-colporate, tectate, spinulose condition.

Erdtman (1952) remarked that the pollen grains of *Roridula dentata* are dissimilar to those in Clethraceae, Ochnaceae, and Pittosporaceae. Tricolporate pollen grains similar to those in *Roridula dentata*, having spinulose tectum, occur in *Corokia* A. Cunn. (Cornaceae) and *Cardiandra* Sieb. & Zucc. (Hydrangeaceae), both in Cornales (see Hideux & Ferguson, 1976), but their tectum is not perforate. Section studies are needed for further conclusions.

Embryology and seed. A careful embryological investigation of *Roridula gorgonias* by Vani-Hardev (1972) provides the following data. The anther walls are 5–6-layered, and the formation is presumably of the Basic type. The endothecium lacks fibrous thickenings (related with the apical, ± poricidal dehiscence), and the tapetum is 1–2-layered, glandular, with cells showing nuclear divisions and fusions. One middle layer (the outer) is tanniniferous, the other consists of compressed cells. Microsporogenesis is simultaneous, and the pollen grains are 2-celled when dispersed.

The ovules are anatropous and have a single, thick integument. Embryo sac formation is of the *Polygonum* type. The nucellar epidermis disintegrates by the time the embryo sac is 2-nuclear, and the embryo sac then comes to lie in direct contact with an integumentary tapetum (endothelium) of palisadelike cells. The embryo sac has a conspicuous hypostase at its chalazal end. The synergids lack hooks. The endosperm formation is cellular, with vertical division of the micropylar cell and with transverse division of the chalazal first cell (type "213" according to the classification by di Fulvio, 1983). No endosperm haustoria are formed. The mature endosperm cells are tannin-rich.

The embryogenesis follows the Solanad type, but embryo formation lags behind endosperm formation. In the mature seed, the embryo is still quite small, whereas the endosperm is copious. The hypostase cells become thick-walled. The seed coat in *Roridula gorgonias* is thick and warty, but not in *R. dentata*.

From these data Vani-Hardev (1972) concluded that *Roridula* should be removed from Droseraceae. The morphological evidence according to the same author did not support a close relationship to *Byblis* either, and Vani-Hardev considered Roridulaceae, Droseraceae, and Byblidaceae as distinct, not particularly closely related families. No conclusions on ordinal re-

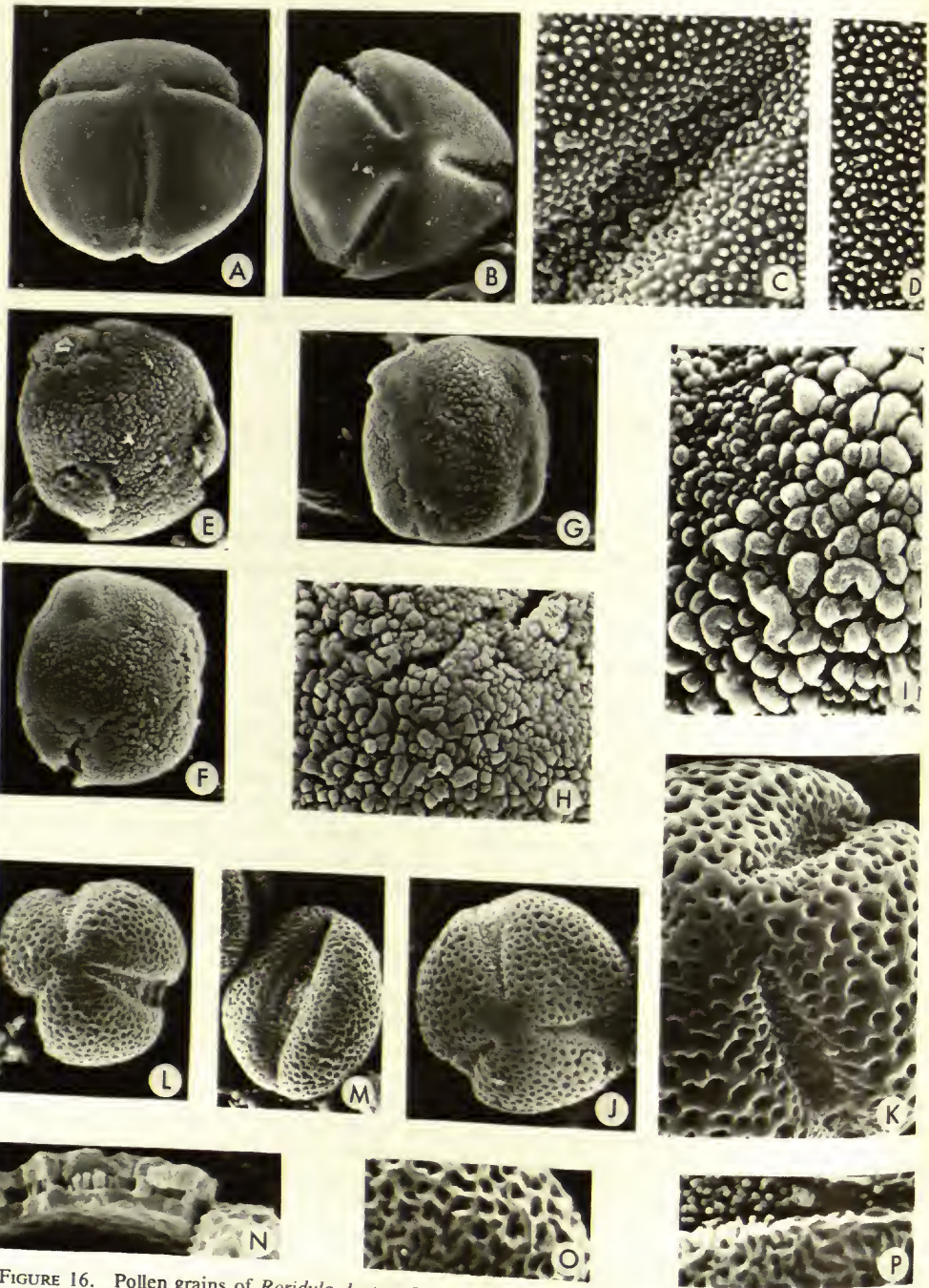


FIGURE 16. Pollen grains of *Roridula dentata* L. (A–D); *R. gorgonias* Planch. (E–I) (both Roridulaceae); *Retzia capensis* Thunb. (Retziaceae) (J, K); and *Stilbe* cf. *ericoides* L. (Stilbaceae) (L–P).—A, B, J–L. Pollen grains, polar and obliquely polar views.—M. Pollen grain in equatorial view.—D, E, O. Details of mesocolpal exine, I bordering in the upper left corner on apertural region.—C, H, P. Details of colpal regions.—E–G. Irregular pollen grains in different views.—N. Broken exine showing thick tectum and nexine and baculae. Magnifications: A, B. ×900; C, D. ×5,000; E, F. ×625; G. ×550; H. ×2,250; I. ×3,750; J. ×1,000; K. ×2,000; L. ×1,300; M. ×1,200; N. ×6,200; O, P. ×3,750. Material: A–D. Alcohol-fixed material collected by P. Goldblatt, Hermanus, Caledon Distr.; E–J. *Dahlgren & Strid 3183* (LD); J, K. *Dahlgren & Strid 3695* (LD); L–P. *Goldblatt 3699* (C). (Preparation and photography by J. Praglowski.)

lationships were presented by Vani-Hardev (1972).

Chromosome number. Kress (1970) and Peng & Goldblatt (1983) both independently reported the chromosome number for *Roridula gorgonias* to be $2n = 12$ ($n = 6$).

Phytochemistry. Schizogenous resin ducts, as found in the bark of members of Pittosporaceae, are absent from *Roridula.* The resin or balsam produced in the heads of the tentacular hairs has apparently not been analyzed. Tannins are present in endosperm cells and also in the integument of the seeds. Calcium oxalate crystal druses occur in the leaf epidermis. Iridoid compounds, not fully identified, have been detected in leaf samples of *R. dentata* (Jensen et al., 1975).

Grund & Jensen (1981), in a serological study using seed proteins from taxa often regarded as members of Saxifragales sensu lato, found considerable serological affinity between taxa of Hydrangeaceae, Cornaceae, and *Roridula* but none between these and Saxifragaceae sensu stricto. It should be noted that the first three families all agree in embryological and seed characters and have taxa containing iridoids. Cornaceae and Hydrangeaceae are placed in Cornales by Dahlgren (1975, 1980a, 1983).

Conclusions and relationships. Past considerations on relationships between *Roridula* and other groups have been based largely on gross morphology, in particular the presence of the conspicuous tentacular hairs. Floral differences between *Roridula, Byblis,* and the genera of Droseraceae have not been considered sufficient to eradiate the impression that these are allied. Present knowledge of the great differences in the construction of the tentacular hairs in the three groups (see Bruce, 1907) in itself indicates that the tentacular hairs have little to do with each other and have evolved independently. In *Roridula* they are not even associated with the formation of proteolytic enzymes.

Vani-Hardev (1972) also pointed out a number of gross morphological differences between *Roridula* and *Byblis.* The floral construction in *Roridula* represents a common and neutral type based on a pentamerous, choripetalous type with alternating whorls of sepals, petals, and stamens, and in itself is concordant with types found in a number of orders, including Cunoniales, Saxifragales, Geraniales, Cornales, Ericales, and Pittosporales. The primitive vessel characters are met with in families of Hamamelidales, Cunoniales, Ericales, Cornales, and several families placed in different orders, such as Bruniaceae, Grubbiaceae, Geissolomataceae, and Daphniphyllaceae (Carlquist, 1976b). It can be noted that families in Cornales often have primitive wood such as encountered in *Roridula.*

Embryological features indicate particular relationships much more clearly. Unitegmic tenuinucellate ovules in combination with cellular endosperm formation are chiefly met within the superorders Corniflorae (incl. Ericales and Cornales), Lamiiflorae, Gentianiflorae (excl. Gentianales with nuclear endosperm formation), Loasiflorae, and Campanulales but are foreign to families such as Saxifragaceae sensu stricto, Cunoniaceae (and related small families), Rosaceae, Hamamelidaceae, Geissolomataceae, and Daphniphyllaceae. Further, iridoid production, seeds with copious endosperm and a small embryo, and vessels with scalariform perforation plates are characteristics that strongly restrict the plausible relationships to Corniflorae (Cornales, Ericales, Sarraceniales). Among these orders, most but not all Ericales (except, for example, Clethraceae) are characterized by having terminal endosperm haustoria, and many members of Ericales have pollen tetrads and mycorrhiza, attributes lacking in *Roridula.* These characters argue in favor of placing Roridulaceae in Cornales sensu Dahlgren (1983). This order includes families such as Sambucaceae and Cornaceae found by Grund & Jensen (1981) to have serological affinity to *Roridula.* Pollen grains somewhat similar to those in *R. dentata* occur in Cornales.

Most characteristics discussed above are also found in Ericales, where anthers with poricidal dehiscence are typical. Ericales are also strongly represented in southern Africa, although mainly by *Erica* and related genera, the wood anatomy of which is unlike that in *Roridula.*

In conclusion, Roridulaceae agree well with the general pattern of characteristics in Cornales. This order is defined to a great extent by the embryological syndrome of unitegmic tenuinucellate ovules, cellular endosperm formation, lack of endosperm haustoria, seeds with copious endosperm, and a small embryo. They also often have iridoid compounds (frequently including seco-iridoids), variable wood anatomy including types with long, primitive vessels with oblique walls having scalariform perforations. The floral characters in Cornales are somewhat variable. The 5-merous haplostemonous type with sta-

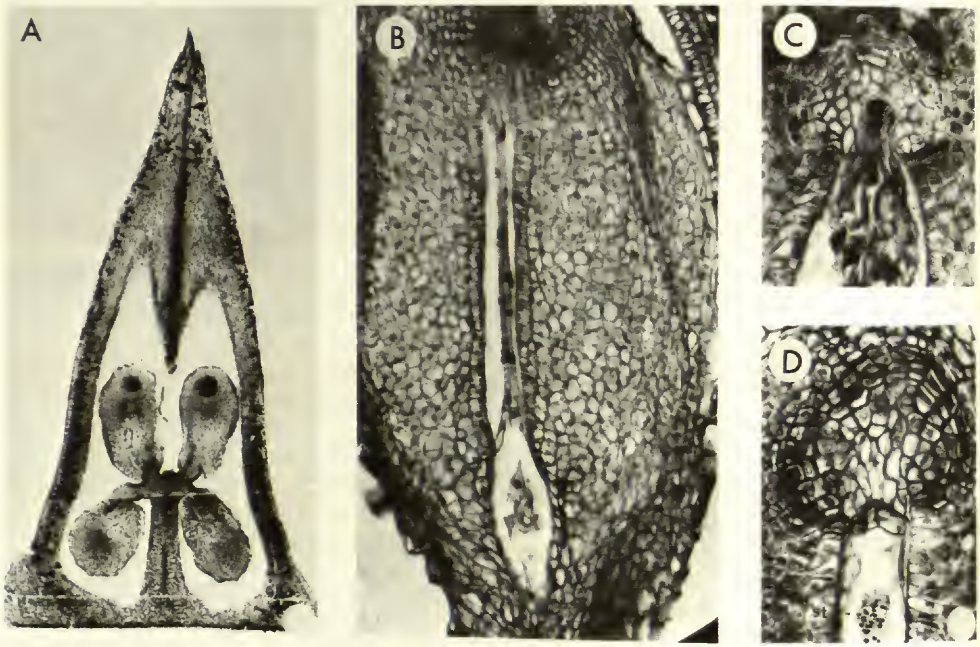


FIGURE 17. *Retzia capensis* Thunb. (Retziaceae).—A. Longitudinal section of ovary showing the incompletely 2-locular ovary with both ascending and pendulous ovules, the ascending here seen with dark-staining hypostase.—B. Ovule during early stage of endosperm formation; the endosperm at this stage is very narrow and cellular; on top is seen the dark-staining hypostase; the endothelium, bordering on the endosperm, is well developed.—C. Hypostase and chalazal endosperm haustorium (dark), dissolving the central contents of the hypostase.—D. Hypostase and upper part of embryo sac at an earlier stage than C; the dark-staining spots are starch grains. (Preparation by K. Engell; FAA-fixed material supplied by I. Williams, from Voëlklip, Hermanus.)

mens opposite the sepals is not uncommon. Families included in Cornales are, for example, Hydrangeaceae, Escalloniaceae, Icacinaceae, Symplocaceae, Cornaceae, Aucubaceae, Alangiaceae, Viburnaceae, Sambucaceae, Adoxaceae, and perhaps also Aquifoliaceae and Montiniaceae (see later text). The relationships within the order and the closest relatives of Roridulaceae within the order are still uncertain and need further study.

It may be added that both Bruniaceae and Grubbiaceae, which are similar in wood anatomy to Roridulaceae, also show some similarities to Ericales and Cornales in embryological features, as far as these are yet known.

RETZIACEAE Bartling

Description. Shrub, sparingly branched, to 1.3 m, evergreen, with stiff, coarse branches densely villous or tomentose on distal (young) parts. Branching monopodial, with lateral (in the upper parts floriferous) short shoots. Branches longitudinally ridged, with distinct, transverse leaf scars. Leaves erect or ascending, in verticels of 3, 4, or 5, three mainly on the thin branches; simple, sessile, entire, exstipulate, linear or narrowly lanceolate, to 40 × 4 mm or, in the floral region, to 50 × 6 mm large, puberulous to white-hairy at least basally and marginally, apically with margins revolute and with a narrow furrow on each side of the prominent midvein. Flowers crowded on multifoliate lateral short shoots, in few-flowered, contracted spikes; each spike with only one or two flowers fully developed at a time. Pedicel short; prophylls 2, narrowly lanceolate, reaching almost as far as the calyx lobes. Flowers large, bird pollinated, bisexual, actinomorphic, 5-merous in calyx, corolla, and androecium, and with a 2-carpellary syncarpous pistil. Calyx tubular-campanulate, puberulous (glabrous below), lobes linear-lanceolate. Corolla to 65 mm long, tubular, bright or orange-red, basally glabrous, distally pubescent; lobes triangular-ovate, dark bluish-black, white-pubescent, basally convolute, otherwise valvate in aestivation. Stamens

5, equal, alternating with the petals; filaments inserted in the corolla tube slightly below the sinuses between the petals; anthers sagittate, introrse, dorsifixed, versatile, 4-sporangiate, obtuse, longitudinally dehiscent, the two thecae basally distant. Pollen grains dispersed as monads. Pistil basally encircled by a narrow, inconspicuous, annular disc. Ovary basally bilocular but apically unilocular (Fig. 17A), the septum not reaching beyond the placenta; this situated centrally a little more than half way up the locules. Ovules 4–6, each locule with one ascending and 1–2 pendulous ovules. Style terminal, filiform, erect, slender, apically bibrachiate, with adaxial stigmatic papillae. Fruit a longitudinally dehiscent, ± folded capsule enclosed in the calyx; dehiscence initially loculicidal from the apex, each valve soon becoming bilobed and also septicidal. Seeds up to 4, to ca. 6 mm long, elongate-triangular, reticulate, somewhat crested; embryo surrounded by mealy endosperm, straight, cylindrical, almost as long as the endosperm (Leeuwenberg, 1964).

General information. Retziaceae consist of the single genus *Retzia* Thunb. with the single species *R. capensis* Thunb. It is restricted to the Somerset West, Caledon, and Bredasdorp districts in the Cape Province (map in Dahlgren et al., 1979), where it grows on mountain slopes at low altitudes, on substrate weathered from Table Mountain Group sandstone, in fynbos vegetation.

Treatment in the literature. The previous history of treatment has been outlined by Goldblatt & Keating (1976) and Dahlgren et al. (1979) and will not be repeated here in detail. The genus has been included in Solanaceae, Convolvulaceae, and Loganiaceae but in later years has often been treated in a separate family placed in either Solanales, Polemoniales, Gentianales, or Scrophulariales.

In recent literature, *Retzia* was included in Loganiaceae (Gentianales) by Leeuwenberg (1964, 1980). A position near Loganiaceae in Gentianales is also supported by Cronquist (1981, 1983) and Thorne (1976, 1981, 1983). Data on cytology and pollen was given by Goldblatt & Keating (1976), who did not find reasons to remove *Retzia* from Loganiaceae. Dahlgren (1975, 1980a, 1983) and Dahlgren et al. (1979) as well as Takhtajan (1980) placed Retziaceae in a separate family in Scrophulariales near Scrophulariaceae and Buddlejaceae. Dahlgren et al. (1979), particularly, stressed the similarities between *Retzia* and genera of Stilbaceae and concluded that these are probably related and should be placed in Scrophulariales. This treatment was contested by Cronquist (1981, 1983) and Thorne (1983).

Embryological information, placed at our disposal by Engell (1987), will be added to other evidence here. Together the information gives a satisfactory basis for a placement of Retziaceae.

Macromorphology. Among the interesting features of *Retzia* are its verticillate, ericoid leaves, which differ considerably from those in most taxa of Scrophulariales, Gentianales, and Solanales. They may have arisen by adaptive evolution in response to the Mediterranean type climate in the Cape (cf. the leaves in many Ericaceae, in Grubbiaceae, etc.). Similar leaves occur in Stilbaceae, but these are not necessarily of a common origin (although possibly so; see Dahlgren et al., 1979).

The adaptation to bird pollination is also a special feature of *Retzia* and is expressed as a syndrome of stiff branches (pollinating birds in South Africa, unlike hummingbirds, are often not able to hover while collecting nectar), large, red and black corolla, pollen exposed at the rim of the corolla tube, and a style protruding from the corolla.

The woodiness, the rather primitive vessels, the actinomorphic flowers with five equal stamens, and the occurrence of a central placenta with ascending as well as pendulous ovules are features indicating that *Retzia* is a primitive taxon, whether placed in the order Scrophulariales or Gentianales.

Anatomy. The anatomy of *Retzia* has been studied in some detail by Herbst (unpubl. data), from which some of the information is taken. Intraxylary phloem is lacking, an indication that *Retzia* is not related to Solanaceae or Convolvulaceae. Vessels with simple perforation plates are mixed with vessels having scalariform perforation plates, the latter more frequent (Herbst, unpubl. data). The scalariform perforation plates have 5–12 bars (Mennega in Leeuwenberg, 1980). The fibers are nonseptate and arranged in regular rows. The rays are uniseriate and 2–5(–7)-seriate; the uniseriate being 1–12 cells high with upright cells, the multiseriate rays having a middle part of 10–16 rows of square or procumbent cells and short to long uniseriate wings (Herbst, unpubl. data).

The leaves have a pronounced ericoid mor-

phology. The stomata are anomocytic and are not particularly sunken. Hairs of two kinds are present: filiform hairs of 1–3 cells, the distal longest; and small, stalked glandular hairs.

Pollen morphology. The pollen morphology was described by Punt & Leenhouts (1967) and by Goldblatt & Keating (1976). The pollen grains (Fig. 16J, K) are isopolar, radially symmetrical, and 3-colporate, prolate-spheroidal, and have a colpus diameter of ca. 34 μm. The exine is tectate, perforate to microreticulate, and the tectum is supported by bacula. The ora are lalongate and have a colpus membrane with granular processes (Praglowski, unpubl. data).

Embryology. According to Engell (1987) the embryology of *Retzia* is as follows. The anther wall epidermis consists of small cells, while those of the endothecium are much larger and nearly isodiametric. The tapetum is glandular. The pollen grains are dispersed in the 2-celled state.

The ovules are anatropous, unitegmic, and tenuinucellate. The integument of the mature ovule is multilayered, and the micropylar canal is very long. An endothelium (integumentary tapetum) of palisadelike cells two to three times as high as broad develops as soon as the nucellar epidermis breaks down, which occurs before the embryo sac is mature. The embryo sac formation is of the *Polygonum* type, but only two antipodals are present. The embryo sac is 8-nucleate. A hypostase (Fig. 17C, D) is formed on the chalazal side of the embryo sac and consists of concentric cell layers around a center of rectangular cells. At fertilization the embryo sac contains numerous starch grains that disappear later. The endosperm formation is basically cellular—strictly cellular in the micropylar and chalazal parts, but in the central chalazal parts of the embryo sac wall formation does not keep pace with nuclear division and the cells in this part may have several nuclei. The micropylar end consists of long, narrow, and vacuolated cells (Fig. 17B). Later, the endosperm becomes entirely cellular and consists of long, narrow cells. Endosperm haustoria are formed; the micropylar one is most distinctive, while the chalazal haustorium dissolves the central cells of the hypostase (Fig. 17C) but is further prevented in its growth by the more thick-walled, concentrically arranged hypostase cells. The seeds are endospermous.

Chromosome number. The chromosome number in *Retzia capensis* is $2n = 12$ (Goldblatt & Keating, 1976).

Phytochemistry. Four iridoid compounds are known in *Retzia* (Dahlgren et al., 1979), all of the carbocyclic type. Seco-iridoids are lacking. Two of the iridoids found are yet unknown in other plants; the other two, stilbericosid and unedoside, are both reported for *Stilbe* (Stilbaceae), unedoside also for *Arbutus* (Ericaceae).

Conclusions and relationships. When discussing the affinities of *Retzia* in the past, the alternatives have been whether it is related to Solanaceae or Convolvulaceae of Solanales, Loganiaceae of Gentianales, or Scrophulariaceae of Scrophulariales (or members of these families). Some confusion in the literature derives from the circumstance that Buddlejaceae are sometimes included in Loganiaceae or placed next to it, in Gentianales (Leeuwenberg, 1964, 1980; Cronquist, 1981, 1983; Thorne, 1981, 1983). Similarities between *Retzia* and members of Buddlejaceae are then referred to as criteria for a position in Loganiaceae or next to this family. In other treatments (Dahlgren, 1975, 1980a, 1983; Takhtajan, 1980), Buddlejaceae are treated as a separate family near Scrophulariaceae in Scrophulariales. Arguments for the latter relationship will be given later. To the aforementioned alternatives may be added a fair concordance between *Retzia* and members of Ericales.

The position of *Retzia* in Loganiaceae, and its treatment as a separate family near Loganiaceae in Gentianales can be dismissed on several grounds. Vessel characters differ from those in all Loganiaceae. (*Desfontainia* Ruiz & Pav., also with scalariform perforation plates, should probably be excluded from Loganiaceae; it also has very different pollen grains, see Hoc & Bravo, 1984.) The kinds of carbocyclic iridoids and the lack of seco-iridoids support a position in Scrophulariales or Ericales but not Gentianales. Punt (1980) regarded the pollen grains of *Retzia* and of the genera presently treated in Buddlejaceae as different from those in true Loganiaceae. Finally, and most convincingly, the embryological features of *Retzia* and Buddlejaceae differ from Loganiaceae and other Gentianales, where presence of hypostase, cellular endosperm formation (with few exceptions and then of a

different kind), and the presence of terminal endosperm haustoria are never recorded. Intraxylary phloem is also lacking in *Retzia* and the Buddlejaceae.

The flowers of Retziaceae are sympetalous and pentamerous with alternating calyx, corolla, and androecium, and with two median carpels, and are compatible with the general features in several ("Sympetalae") orders, although the position of the carpels is not in accordance with the condition in Solanaceae. The embryological syndrome shown above (Engell, 1987) accords with Ericales of the Corniflorae (sensu Dahlgren, 1983) and Lamiales and Scrophulariales of the Lamiiflorae (the last two orders are best united). Presence and type of carbocyclic iridoids are indicative of exactly the same orders (unedoside known in Ericaceae and Stilbaceae, stilbericoside in Stilbaceae). Although Ericales are generally not associated with the Lamiiflorae (because of mycorrhiza, common obdiplostemony, more carpels, etc., in Ericales), the relationships between the orders are probably closer than usually acknowledged.

Indeed *Retzia* differs from most Scrophulariales in having actinomorphic flowers, five equal stamens, and both vessels with simple and scalariform perforation plates. These features are all, however, considered to be primitive (plesiomorphic) in the order; each does occur, exceptionally, in other families. The chromosome number ($2n = 12$) in *Retzia* is compatible with that in Scrophulariaceae, for which Raven (1975) postulated a chromosome base number of $x = 7$, many taxa having $2n = 12$ or $2n = 14$. Buddlejaceae contrast in having $x = 19$.

The embryological features of *Retzia* show great concordance with *Buddleja* L. (K. V. O. Dahlgren, 1922; Bendre, 1975) but also with some genera of Scrophulariaceae, e.g., the woody genus *Oftia* Adans. (De Vos, 1963), all having a hypostase, cellular endosperm formation, and terminal endosperm haustoria.

Because of the almost actinomorphic (but 4-merous) corolla, the genera of Buddlejaceae (*Buddleja, Peltanthera* Benth., *Sananango* Bunting & Duke, *Nuxia* Lam., *Androya* H. Perrier, *Gomphostigma* Turcz., and *Emorya* Torr.) have often been associated with *Retzia*. As far as is known, embryological details such as the elongate embryo sac and endosperm cells, the development of endosperm haustoria, and presence of hypostase are similar. Pollen grains in some species of *Buddleja* are also similar to those in *Retzia* (Punt, 1980).

Similarities between *Retzia* and the Stilbaceae, a family of five small genera (12 spp.) restricted to the Cape, were emphasized by Dahlgren et al. (1979) (see later text). The woody habit, the presence of vessels with scalariform perforation plates, the general leaf morphology, the pollen grains (which agree surprisingly well with those in *Retzia* in details such as the microreticulate exine and the granular colpus membrane), and the iridoid contents are all conspicuous similarities.

In conclusion, *Retzia* is here considered a distinct family not closely related to Solanales or Gentianales but rather (though distantly) to Ericales and, especially, Scrophulariales–Lamiales. Within the last-mentioned complex, *Retzia* stands out as having a number of primitive (plesiomorphic) character states and in this sense forms a "relic" element (although it is advanced with respect to bird pollination). Most similarities are with the families Stilbaceae, Scrophulariaceae (some woody genera), and Buddlejaceae; Retziaceae are best placed among these, in Scrophulariales.

Stilbaceae Kunth

Description. Erect or ascending, sympodially branched shrublets (all woody), with young branches hairy or glabrous, divided into longitudinally rectangular sections, one below each leaf, separated by furrows. Leaves densely set, usually verticillate (in whorls of 3–7), rarely opposite, simple, entire, ± pointed, exstipulate, elongate, lanceolate to linear, "ericoid" (with stiff texture, revolute margins), often S-curved or boat-shaped, often triquetrous in transection, glabrous or adaxilly ± pubescent. Inflorescence spicate, pauciflorous to multiflorous, each flower supported by a bract similar to but often broader than the foliage leaves, and often pubescent. Flowers sessile, with two basal, relatively large, convex bracteoles (prophylls); these never with axillary flowers. Flowers basically 5-merous, bisexual, hypogynous, synsepalous, sympetalous, with 4 stamens (the median rarely present as a staminode) and a 2-carpellary pistil. Calyx tubular, regularly 5-lobate or (*Xeroplana* Briq.) somewhat bilabiate, glabrous or pubescent. Corolla regular or (*Xeroplana* and *Eurylobium*

Hochst.) clearly zygomorphic, glabrous or (usually) variably pubescent within the throat only (Rourke, 1977); tube narrowly funnel-shaped; lobes 5 or (*Campylostachys* Kunth) 4(–6), imbricate, the upper in zygomorphic flowers broader than the lower and fused mutually to a higher level. Stamens 4, inserted in the throat of the corolla tube between the lobes, incurved in bud; filaments linear, often as long as or longer than the petal lobes; anthers ovate to elongate, dorsifixed, 2-thecate, 4-sporangiate, sometimes slightly sagittate, longitudinally dehiscent. Pollen grains dispersed singly. A narrow, indistinct to obsolete disc present around ovary base. Ovary 2-locular, but one locule always empty; septum between locules sometimes incomplete (Dyer, 1975). Fertile locule with 2 basal-axile, erect, anatropous ovules. Style apical on ovary, never sunken, filiform, often slightly dilated in distal half, with punctiform undivided stigma. Fruit dry, indehiscent or dehiscent (capsular). Seeds reticulate.

General information. The family consists of five genera: *Stilbe* Berg. (six spp.), *Campylostachys* Kunth (two spp.), *Xeroplana* Briq. (two spp.), *Eurylobium* Hochst. (one sp.), and *Euthystachys* A. DC. (one sp.). The distribution is restricted to the winter rainfall regions of the Cape Province and extends between the Cape Peninsula and the Uitenhage district, with nearly all species west of Riversdale.

Treatment in the literature. Stilbaceae ("Stilbeaceae") have, since being described by Kunth (1831), generally been included in Verbenaceae as a subfamily or tribe. Lindley (1853) and Hutchinson (1969) both acknowledged the family as distinct, Lindley placing it in Gentianales, and Hutchinson in Verbenales. Verbenales was distinguished by Hutchinson as the woody counterpart of his Lamiales. Stilbaceae were included in Verbenaceae by Phillips (1951) but treated as a separate family by Dyer (1975). Dahlgren (1980a, 1983) acknowledged Stilbaceae on the basis of the similarities between its members and *Retzia* Thunb. as well as members of Scrophulariaceae and Buddlejaceae demonstrated in Dahlgren et al. (1979), in which account two iridoid compounds shared between *Stilbe* and *Retzia* were reported. The conclusion was criticized by Cronquist (1981, 1983), who includes Stilbaceae in Verbenaceae and Retziaceae in Loganiaceae.

Macromorphology. The Stilbaceae are usually included in Verbenaceae because of the gynoecial structure: the fertile locule has two basal, ascending, anatropous ovules. This character is by no means present in all other Verbenaceae, in which the position of the ovules varies much, from the central or even upper part of the septum to the basal position. A reduction of ovule number to two or one per locule is found also in other Scophulariales–Lamiales. It should be pointed out here that Scrophulariales cannot be distinguished from Lamiales; the latter have apparently evolved within Scrophulariales (Lu, in press). A complete abortion of ovule(s) in one of the locules of the ovary, resulting in one fertile and one empty (often indistinctly discernible) locule, has obviously evolved independently in other taxa of Scrophulariales–Lamiales. One example is *Phryma* L. (Phrymaceae, often likewise included in Verbenaceae). Another is Globulariaceae, a small family of two genera in Macaronesia, the Mediterranean, temperate Europe, southwestern Asia, and northern and northeastern Africa. A third example is part of the tribe Selagineae of Scrophulariaceae, viz., the genera *Microdon* Choisy, *Gosela* Choisy, *Agathelpis* Choisy, and *Globulariopsis* Compt. Other Selagineae have both locules fertile, with one pendulous ovule in each locule. Similar to Selagineae are genera of the Manuleae of Scrophulariaceae. The variation in these tribes includes forms with numerous ascending and pendulous ovules: in *Tetraselago* Junell (see Junell, 1961) with one pendulous and one erect ovule in each locule (as in, e.g., *Retzia* Thunb.); with one pendulous ovule per ovary; and others with one pendulous ovule in one of the two locules only. Cronquist (1981) includes the Selagineae in his Globulariaceae, but it is not yet clear that these are directly related.

Anatomy. It will only be noted here that Metcalfe & Chalk (1950) report that glandular hairs with a very small, one- or few-celled head occur in Stilbaceae (as in Retziaceae).

Pollen morphology. As is remarked under Retziaceae, the pollen grains of *Retzia* agree fairly well with those in Stilbaceae (J. Praglowski, unpubl. data) (Fig. 16L–P). The pollen grains of *Stilbe* cf. *ericoides* L. are isopolar, radially symmetrical, 3-aperturate (presumably 3-colpate, as ora are not discernible), prolate-spheroidal and rather small (polar axis ca. 22 μm, equatorial diameter ca. 20 μm). The exine is tectate, with

the tectum supported by infratectal bacula. Tectal perforations are minute and located within pits, giving the tectum a microreticulate appearance. The colpi are relatively wide and have a colpus membrane with granular processes that are most concentrated in the equatorial area.

As remarked by Dahlgren et al. (1979), the pollen grains of Stilbaceae and *Retzia* show similarity. It needs to be pointed out (Fig. 16) that the outline, the exine sculpture, and the granular surface of the colpus membrane are conspicuously similar. Erdtman (1952) reported the pollen of *Stilbe* to be tricolporate, but this is not distinct or visible in the colpus of the single taxon of our study.

Embryology and seed. No information is available here. However, as the question regarding the affinity of the Stilbaceae is largely confined to groups *within* the Scrophulariales–Lamiales, the basic type is expected to be more or less the same. The seeds in Stilbaceae are reported to be endospermous, whereas those in Verbenaceae are generally exendospermous (Emberger, 1960).

Chromosome number. No information.

Phytochemistry. See under Retziaceae. The co-occurrence of two particular carbocyclic iridoids, stilbericoside and unedoside (see Dahlgren et al., 1979), in Stilbaceae and Retziaceae has been one of several arguments for considering these families rather closely related.

Conclusions and relationships. The Stilbaceae have a basic position within Scrophulariales–Lamiales with several features plesiomorphic within that order. The features that knit Stilbaceae to Verbenaceae are chiefly the two basal, erect ovules (only one locule fertile in Stilbaceae). However, the ovular position is not constant in Verbenaceae sensu stricto, and the argumentation for including Stilbaceae in this family is weak and inconclusive.

On the other hand, as shown by Dahlgren et al. (1979), there are a number of similarities between Stilbaceae and Retziaceae (*Retzia* Thunb.), although the latter have large, bird-pollinated flowers and the former have small, insect-pollinated flowers. A combination of anatomical, morphological, pollen morphological, and iridoid-chemical features supports the concept of a close relationship between these two small families. The geographical concentration in the same region adds credence to this supposition.

The Stilbaceae, in our view, should be treated as a distinct family in Scrophulariales (incl. Lamiales) and placed next to Retziaceae, Scrophulariaceae, and Buddlejaceae.

Lanariaceae
Huber ex Dahlgren, fam. nov.

Description. An erect, tough, 40–80 cm tall herb with relatively short, vertical or almost vertical rhizome whitish in transection (Fig. 18). Lower parts of rhizome dark, verrucose, with one rather thick root emerging from each wartlike lobe; upper part of rhizome bearing several leaves and, below these, a coat of densely set, fibrous, brownish black sheaths of old leaves. Old roots remaining as firm fiber cords. Radical leaves spirally arranged, dorsiventral, linear, sheathing at base, to >30 cm long, dull green, stiff, glabrous (or subglabrous), with ca. 9 prominent parallel veins; when dry the margins incurved and then appearing subterete. Flowering stem usually with 1–2 green foliole leaves below the inflorescence, these green, similar to but shorter than radical leaves, and basally pubescent; the stem with white, plumose hairs above, increasingly dense on distal parts and on the inflorescence, this appearing white-wooly. Inflorescence a much-branched, bracteate corymb or expanded panicle, consisting (according to Pax & Hoffmann, 1930) of cincinnal components. Flowers small, bisexual, with 6 equal tepals fused into a cylindrical-infundibular tube; this free from the pistil base (stipe and ovary base) but attached to the ovary laterally to somewhat below the ovary apex (Fig. 18F). Perianth densely plumose pubescent abaxially; tepals lanceolate, subobtuse, about as long as the tube; glabrous adaxially, smooth, mauve. Stamens 6, inserted at mouth of the tube, slightly shorter than the perianth; filaments erect, subfiliform; anthers dorsifixed, epipeltate, versatile, introrse, 2-thecate, 4-sporangiate, basally sagittate, dehiscing by longitudinal slits. Pollen grains dispersed singly. Pistil trilocular with a terminal, erect, slender, subfiliform style reaching as far as the tepals, apically trilobate, with small stigmas. Locules each with 2 basal, axile, anatropous ovules. Fruit a one-seeded capsule, the fertile locule dehiscing loculicidally. Seed single, black, shiny, with thick testa encrusted with

FIGURE 18. *Lanaria lanata* (L.) Durand et Schinz.—A. Basal part of stem.—B. Upper part of stem and inflorescence.—C. Flower.—D. Hair from upper part of stem.—E. Flower, longitudinal section.—F. Ovary, longitudinal section; the basal as well as upper part of the ovary is free from the hypanthial tube. *Ecklon & Zeyher*, "Tulbagh Waterfall" (C).

phytomelan (Huber, 1969). Endosperm copious, nonstarchy; embryo linear.

Planta erecta, plerumque 40–80 cm alta. Rhizoma verticalis, apicaliter tunicata. Folia rosulata dorsiventrales, lineares, ca. 9-nervosi, vaginantes, glabra vel subglabra. Caulis erectus, plerumque bifoliatis, distaliter densissime lanatus; pili plumosi. Inflorescentia dense plumoso-pubescens, corymbosa, rhipidiis composita. Flores hermaphroditi, actinomorphi, syntepali; tubus perianthii cylindricus–anguste infundibuliformis; lobi lanceolati. Perigonium extra plumoso-lanatum, intra glabrum roseum. Stamina 6, aequales; antheris introrsibus, dorsifixis, longitudinaliter dehiscentibus. Ovarium 3-loculares, lateraliter tubo perigoni adnatum; stylus singularis, rectus, apicaliter 3-brachiatus; loculi biovulati. Ovulae centrales, anatropi. Embryologia cum Tecophilaeaceae. Capsula 1-seminalis, loculicida. Semen phytomelaniferum; endospermum non-amylaceum.

TYPE: *Lanaria lanata* (L.) Durand & Schinz.

General information. Lanariaceae consist only of the genus *Lanaria* Ait., with the single species *L. lanata* (= *L. plumosa* Ait.). It is re-

stricted to the Cape Province, where it occurs from the Hottentots Holland Mountains (Somerset West District) to near Port Elizabeth, and in the northwest to the Tulbagh District. It grows in sand weathered from Table Mountain sandstone, in fynbos vegetation, at low or moderate altitudes.

Treatment in the literature. *Lanaria* has generally been placed in Haemodoraceae (or, where this family has been incorporated in Amaryllidaceae, in the latter) since Bentham & Hooker (1883). The Haemodoraceae have frequently been confused with the Tecophilaeaceae, although these two families are not at all closely related. Following Dahlgren et al. (1985), Haemodoraceae make up the order Haemodorales, having nonphytomelaniferous seeds, starchy endosperm, paracytic stomata, and complex hairs. Tecophilaeaceae are included in Asparagales, a large and variable order, the capsule-fruited taxa of which have phytomelaniferous seeds, nonstarchy endosperm, mostly anomocytic stomata, and only rarely complex hairs (e.g., Hypoxidaceae).

Pax & Hoffmann (1930) thus placed *Lanaria* in the chiefly Australian tribe Conostylideae (of Amaryllidaceae), which in current classifications makes up about half of the Haemodoraceae. *Lanaria* agrees with this tribe in having six functional stamens and branched hairs. Within Haemodoraceae, *Lanaria* is otherwise sometimes placed together with the South African genus *Dilatris* Berg. in the tribe Haemodoreae, with which it agrees in having sulcate pollen grains (e.g., Marloth, 1915). The resemblance between *Lanaria* and *Dilatris,* which are sometimes associated in nature, is probably the reason why the relationships of *Lanaria* have seldom been critically examined. Erdtman (1952), who placed *Lanaria* in Amaryllidaceae subfam. Hypoxidoideae tribe Conostylideae, found that the sulcate pollen grains agree best with tribe Conantherae, now placed in Tecophilaeaceae.

De Vos (1963), in an embryological study, demonstrated that *Lanaria* is embryologically in better agreement with genera of Tecophilaeaceae (e.g., *Odontostomum* Torr., *Cyanella* L.) than with the genera of Haemodoraceae she examined. She questioned seriously its position in Haemodoraceae. Long before that, Schulze (1893) had observed that *Lanaria* (and *Lophiola* Ker-Gawl., now Melanthiaceae) has anomocytic stomata, while other genera treated in Haemodoraceae have paracytic stomata, another feature that would support the exclusion of *Lanaria* from Haemodoraceae.

Hutchinson (1959, 1969), Dyer (1976), and Bond & Goldblatt (1984) still placed *Lanaria* in Haemodoraceae. Takhtajan (1980) excludes *Lanaria*, with hesitation, from Haemodoraceae but does not mention it under any other family. On the basis of seed characters, Huber (1969) considered *Lanaria* distinct and worthy of family rank, although the family Lanariaceae was not formally established. Dahlgren & Clifford (1982) and Dahlgren et al. (1985) with some misgivings placed *Lanaria* in Tecophilaeaceae. Zavada et al. (1983) and Simpson (1983), on pollen morphological grounds, excluded *Lanaria* from Haemodoraceae and pointed to a greater similarity with Tecophilaeaceae. Simpson (1983) also noted that *Lanaria* differs from other genera of Tecophilaeaceae in lacking opercular exine.

The position of *Lanaria* still requires resolution. Although similar in habit and some conspicuous features to Haemodoraceae, the genus is clearly unrelated to this family in various microscopic characters. Several features also make *Lanaria* aberrant in Tecophilaeaceae (see Anatomy). The basis for a position in a separate family will be discussed later.

Anatomy. According to Scharf (1892) the stem is differentiated into a cortex and central cylinder, the latter comprising numerous vascular bundles, except in the center, which consists of thin-walled cells. Cheadle (1968) reported that vessels are restricted to the roots and have scalariform perforation plates.

The upper parts of the stem and the inflorescence are closely covered with plumose hairs (illustrated by Schulze, 1893). The hairs arise on a one- or two-celled base of epidermal cells and consist of a multicellular column of elongated cells, each prolonged into a long, thick-walled lateral arm. They are of variable size, small and large being mingled. The larger cauline leaves, which are mainly glabrous, are sparsely clothed below with rather long simple hairs. This hair dimorphism has not previously been reported for *Lanaria* in the literature.

The leaf epidermis, according to Scharf (1892), consists of thick-walled cells, comprising long cells and short stone cells. Stomata were reported by Scharf to occur almost only on the lower side, to be slightly sunken in the epidermis, and to resemble those in *Anigozanthos* Labille (Hae-

modoraceae (i.e., paracytic); but Schulze (1893) claims that the subsidiary cells of the stomata are not or are only slightly different from the other epidermal cells and the stomata thus anomocytic. The parenchyma cells of the leaves contain scattered sacs or cells filled with brown mucilage, but lack crystals, although thin-walled cells surrounding the vascular bundles contain quadrate-octahedric oxalate crystals (Scharf, 1892). Thus raphides seem to be lacking.

Pollen morphology. The pollen grains of *Lanaria* (Simpson, 1983) are tectate with supporting bacula and sulcate, with a thick foot layer and a thick tectum connected by columellae that are more or less constricted or noncoherent at their center. The surface is foveolate and perforate in the nonapertural parts, psilate in the apertural. The aperture is free of exine. The nonapertural wall has two-layered intine, while the apertural intine is thick, three-layered and porous-sinous in structure (Simpson, 1983).

In these characters the pollen grains of *Lanaria* contrast strongly with Haemodoraceae, which have atectate and either monosulcate with apertural exine (tribus Haemodoreae) or 2–8-foraminate (tribus Conostyleae) grains. The pollen grains of *Lanaria* resemble more closely those of Tecophilaeaceae, which, however, have an operculate sulcus. The sulcate, tectate-columellate pollen type with inoperculate sulcus should be regarded as an unspecialized kind of pollen in the Liliiflorae and in itself gives no clear indication of relationships.

Embryology. The embryology of *Lanaria* was studied by De Vos (1963), from which the following data are taken. Microsporogenesis is simultaneous, and in the young pollen grains the generative cell is spindle-shaped to elliptic. The pollen grains are dispersed in the two-celled stage. The tapetum is secretory, with two- to several-nucleate tapetal cells, or later, by nuclear fusions, one- and large-nucleate.

The ovules are anatropous and bitegmic, with a 5-layered (or more) outer integument longer than the largely 2-layered inner integument. A small process at the funicle base was interpreted by De Vos as an obturator and resembles a similar structure found in *Odontostomum* Torr. of Tecophilaeaceae reported by Cave (1952). The micropylar canal formed by the outer integument is not quite opposite the one formed by the inner integument, so the micropyle is zigzag. A parietal cell is cut off from the archesporial cell and forms a parietal tissue, and periclinal divisions also occur in the epidermis at the nucellar apex. The megaspore mother cell is thus covered by a tissue of four or more cell layers. Embryo sac formation is of the *Polygonum* type. The lateral nucellar tissue, at the stage of the 8-nucleate embryo sac, has been absorbed; but the nucellus remains as an apical cap, particularly on the chalazal side of the embryo sac. Endosperm formation is helobial.

Only one of the six ovules of the ovary develops into seed. The seed coat consists mainly of the outer integument, and has thick-walled, palisadelike epidermal cells, which ultimately become encrusted with phytomelan (Huber, 1969). Below the epidermis the testa consists of ca. six more cell layers, while the two cell layers of the inner integument become strongly compressed (De Vos, 1963). The seed is black and shiny. The embryo is slightly curved and about half as long as the nonstarchy endosperm tissue (De Vos, 1963; Huber, 1969).

Most of the embryological features agree with those in Tecophilaeaceae (*Odontostomum, Cyanella* L.), but the embryo sac is wider than in this family. Helobial endosperm is reported for *Odontostomum,* while *Cyanella* is reported to have nuclear endosperm formation (as *Cyanastrum* Oliv., Cyanastraceae). A multilayered testal part of the seed coat, as in *Lanaria,* is also typical to Tecophilaeaceae (incl. the genus *Walleria* Kirk; see later text) and Cyanastraceae but not for, e.g., Hypoxidaceae or Eriospermaceae. Simultaneous microsporogenesis in combination with helobial endosperm formation occurs in Asphodelaceae, Ixioliriaceae and Tecophilaeaceae, all of which also have anatropous ovules and phytomelaniferous seeds. It should finally be added that the embryological characteristics of *Lanaria* exclude any likeness for a close relationship to Haemodoraceae, which lack phytomelan in the seed coat and have a better-developed tegminal seed coat layer, starchy endosperm, orthotropous ovules, and amoeboid tapetum.

Chromosome number. Unknown.

Phytochemistry. Largely unknown. Crystals, presumably of calcium oxalate, and of quadrate octahedral shape, occur in the leaf tissues associated with the leaf veins. Chelidonic acid is reported in *Lanaria* (Hegnauer, 1963). Its occurrence is common in Haemodorales as well as in many families of Asparagales and in this case is of little phylogenetic importance.

Conclusions and relationships. As shown above, *Lanaria* differs conspicuously from the Haemodoraceae, especially in embryology and pollen morphology. These and the seed characters instead argue strongly for a close relationship to families in Asparagales sensu Dahlgren et al. (1985). Among the families with which *Lanaria* can be most closely associated are Tecophilaeaceae, Cyanastraceae, Asphodelaceae, Ixioliriaceae, and Hemerocallidaceae.

Tecophilaeaceae is the family in which *Lanaria* has recently been placed most often, apart from Haemodoraceae. The similarities with this family have also been stressed repeatedly earlier. There are, however, several features in *Lanaria* that are foreign in Tecophilaeaceae as presently circumscribed: 1) the underground parts consist of an elongate rhizome (most Tecophilaeaceae have a corm); 2) the leaves are tough and sclerenchymatous (in Tecophilaeaceae generally mesomorphic); 3) the stems and inflorescences are covered with white plumose hairs (in Tecophilaeaceae such hairs, and generally all kinds of hairs, are lacking); 4) the inflorescence is a corymb with rhipidial lateral units (in Tecophilaeaceae the inflorescence is racemose); 5) the flowers are actinomorphic, with six equal anthers (most Tecophilaeaceae have reductions in the androecium); 6) the anthers dehisce by longitudinal slits from apex to base (in Tecophilaeaceae the anthers dehisce by apical pores or short apical slits); 7) the aperture of the pollen grains is inoperculate (in Tecophilaeaceae operculate). These differences are considered significant enough to exclude *Lanaria* from Tecophilaeaceae, which would otherwise be a very poorly defined family.

The Asphodelaceae include rhizomatous taxa with actinomorphic flowers but are otherwise very different from *Lanaria* in such characters as habit, inflorescence, fusion between perigonal tube and ovary, and pubescence. Yet the family is considered here to be one of the most closely related to *Lanaria* (and the Tecophilaeaceae).

Cyanastraceae are very specialized in seed characters and probably have evolved parallel to the Tecophilaeaceae. They show no greater similarity to *Lanaria* than to the genera of the latter family.

Hemerocallidaceae and Ixioliriaceae, both small, mainly Asian families, show similarities chiefly to the Asphodelaceae and are not considered as likely to be close to *Lanaria.*

Thus *Lanaria,* in our opinion, forms a very distinctive unit and should be treated in a separate family, Lanariaceae, which probably has its closest relatives near Tecophilaeaceae and Asphodelaceae. Tests for anthraquinones in *Lanaria* may be of interest in its possible relationship to the latter of these families.

Tecophilaeaceae Leybold subfam. Wallerioideae Dahlgren, subfam. nov.

Description. Perennial, tuberous, usually 20–60 cm tall, erect, glabrous herbs with a leafy stem (see Fig. 19). Tuber situated ca. 10–15 cm underground, often rather large (to >4 cm across), irregularly globose, untunicated, lobate (with a fibrous root from each lobe), pale in transection, starchy, edible, with apical growing point. Basal underground part of stem with one or more transverse scars after the first cataphylls. Aerial stem ± straight, leafy, with cauline leaves successively larger and more foliose upwards. Stem rigid, smooth, scabrid from inconspicuous hooks present on longitudinal ridges. Leaves all dispersed on the stem and separated by distinct internodes, spirally set, flat, dorsiventral, mesomorphic, nonpetiolate, rarely almost amplexicaul, from linear and ± grasslike (*Walleria nutans* Kirk) to broadly lanceolate or ovate, parallel-veined, the midrib on lower side generally scabrid, with recurved hooks, apically almost to distinctly cirrhous. Flowers solitary in leaf axils, pedicels long, slender, scabrid; a dorsal, green prophyll present on the pedicel close to the flower, at least in *W. nutans.* Flowers stellate, bisexual, actinomorphic, nearly hypogynous, trimerous, pentacyclic. Tepals 6, lanceolate, acute, white, pink, or light blue, unpatterned, basally united in a short tube. Stamens 6; filaments short, erect, inserted in the short floral tube; anthers long, tapering, sometimes laterally coherent, basifixed, yellow/blue or yellow/blue/yellow from base to apex, dehiscing apically by narrow pore or an apical pore continuing in a short slit. Pollen grains dispersed singly. Ovary largely superior, subglobose, smooth, trilocular, each locule with 4–12 ovules on a basal-axile placenta, septal nectaries generally absent, but present as small septal glands in *W. nutans* (Sterling, 1974). Style apical, straight, erect, with apical, punctiform, unbranched stigma. Ovules campylotropous to anatropous. Fruit a globose, slightly 3-lobate capsule (? or berry), generally with 2 or 3 seeds. Seeds rounded-oblong, dark, warty to papillate, each papilla crowned by a tuft of minute hairs.

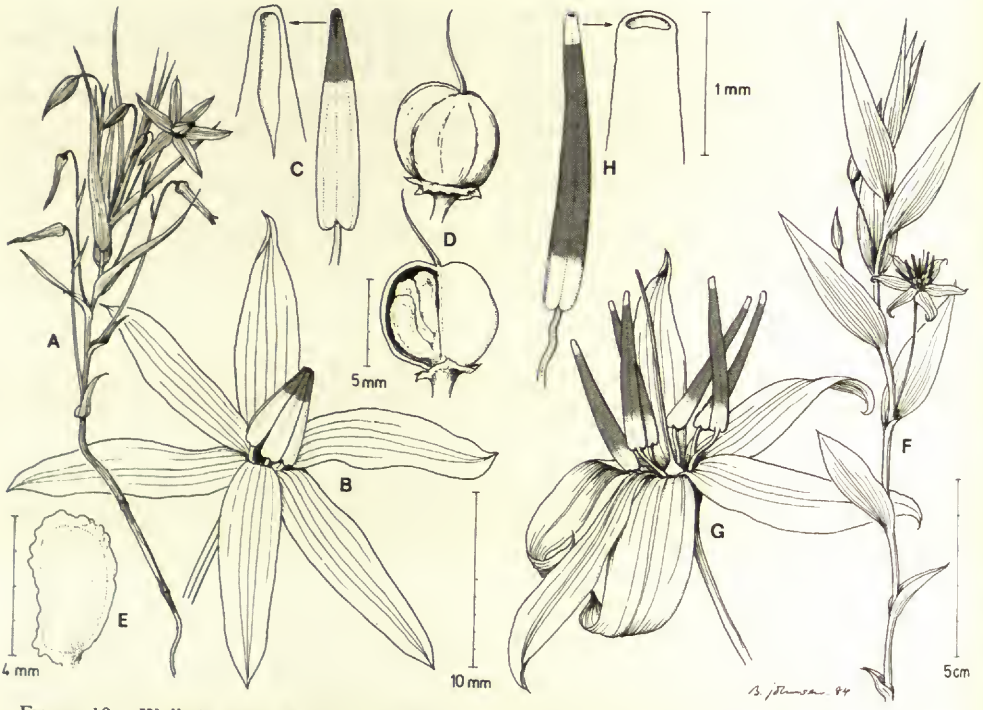


FIGURE 19. *Walleria nutans* Kirk (A–E) and *W. mackenzii* Kirk (F–H) (Tecophilaeaceae subfam. Wallerioideae).—A, F. Whole plants.—B, G. Flowers.—C, H. Stamens and anther apices (note difference in pore shape).—D. Young fruit.—E. Unripe seed. Material: A–E. *Fries, Norlindh & Weimarck 3713* (LD). F–H. *Strid 2538* (C).—Del. B. Johnsen.

Planta tuberifera, erecta, cauli foliosa. Tuber pallidum, globosum, lobatum, amylaceum. Folia basalia bracteosa; folia aliter foliosa, dorsiventralia, sessilia, basaliter vaginata, ovata–linealia, cirrhosa. Caulis et costae foliorum uncinata. Flores solitarii, axillares, hermaphroditi, actinomorphi, subhypogyni. Tepala 6, subaequalia, lanceolata, acuta, alba, rosea vel caerulea. Stamina 6, aequales; filamenta brevia; antherae longae, caeruleae atque luteae, poris terminalibus rotundatis vel elongatis dehiscentes. Ovarium subglobosum, 3-loculare; loculi 4–12-ovulati; stylus singularis, rectus, apicaliter punctiformis. Ovulae campylotropi. Capsula; semina reniformia, non-phytomelanifera, verrucosa, testa multi-strato. Apices verrucae fasciculis trichomatis. Embryo aliquantum magnus.

Typus subfamiliae = typus *Walleriae* J. Kirk.

General information. The subfamily consists of the genus *Walleria* Kirk, with ca. three species in tropical and southern Africa and on Madagascar. According to a revision of *Walleria* by Carter (1962), only three species should be acknowledged: *W. mackenzii* Kirk (incl. *W. angolensis* Baker), *W. nutans* Kirk (incl. *W. hockii* de Willd.), and *W. gracilis* (Salisb.) Carter (incl. *W. armata* Schltr. & Krause), only the last-mentioned of which occurs in the Cape Province, in the Clanwilliam–Namaqualand districts.

Treatment in the literature. Bentham & Hooker (1880) and Baker (1897) placed *Walleria* in Liliaceae subfam. Melanthoideae tribe Uvularieae, together with *Gloriosa* L., *Littonia* Hook., and *Sandersonia* Hook., which was logical in view of its habit (erect, leafy stem; solitary axillary, long-pedicellate flowers; cirrhous leaves) and "tuberous root-stocks." *Walleria* was also placed in the same tribe, together with the same three genera and *Kreysigia* Reichb., *Schelhammera* R. Br., *Uvularia* L., and *Tricyrtis* Wall., by Engler (1888) in the first edition of *Die natürlichen Pflanzenfamilien* but was completely ignored by Krause (1930) in the second edition of the same work. Hutchinson (1934) first kept *Walleria* in the tribe Uvularieae of Liliaceae, with an alternative place in Liliaceae tribus Dianelleae, but later (Hutchinson, 1959) assigned it to Tecophilaeaceae, demonstrating his uncertainty about its relationships. Takhtajan (1980) placed *Walleria*

in a separate tribe, Wallerieae, in Tecophilaeaceae but was hesitant about its position. Thorne (1983) did not mention the genus, and Cronquist (1981) included both Tecophilaeaceae and Colchicaceae in his Liliaceae sensu lato, where *Walleria* is probably placed too, but did not mention the genus either. Dyer (1976), Carter (1966), and Bond & Goldblatt (1984) all included *Walleria* in Tecophilaeaceae.

Huber (1969), in studying the seed structure of the Liliiflorae, introduced the distinction between the "asparagoid Liliiflorae" (= Asparagales) and "colchicoid Liliiflorae" (= Liliales). Tecophilaeaceae with their phytomelaniferous seeds in this classification are clearly asparagoid, while the Uvularieae (incl. *Gloriosa* and *Littonia*) belong in Colchicaceae and are colchicoid. *Walleria* probably lacks phytomelan in the seed coat and has several vegetative features in common with Colchicaceae, but Huber (1969) suggested that *Walleria* should be placed in a distinct family related to Tecophilaeaceae, Cyanastraceae, and Eriospermaceae within the asparagoid group.

Sterling (1974) analyzed the ovary morphology, and in his conclusive remarks stated that "*Walleria* is probably not related to the Wurmbaeoideae but to the Conanthereae, with closest affinity to *Cyanella* or *Tecophilaea*." Dahlgren & Clifford (1982) and Dahlgren et al. (1985) treated *Walleria* in Tecophilaeaceae with reservations.

Macromorphology. Few additions need to be made to the description above.

The tuber in *Walleria* is quite different from the tunicated corm in, for example, *Cyanella* and *Conanthera,* which is regularly globose in outline with the roots concentrated at the base.

The fairly large tubers of *Walleria* are starch-rich and edible, as is the case with those of some species of *Eriospermum.* They are somewhat lobate and, as in *Lanaria,* one root emerges from the apex of each lobe.

One notable condition with *Walleria* is the leaf development, where the first leaves (underground) are bracteate (cataphylls) and the upper cauline leaves, including those of the inflorescence regions, are well developed, large, foliose, and cirrhous. In Tecophilaeaceae the larger leaves are normally concentrated near the base of the aerial stem (although they are not rosulate, as in Eriospermaceae) and decrease in size towards the apical raceme, the upper (subtending the basal flowers or inflorescence branches) being small, foliose or bracteose. Thus the inflorescence in *Walleria* does not consist of unifloral lateral inflorescences but of a foliose, several-flowered raceme.

Anatomy. Cheadle & Kosakai (1971) report that in *Walleria* vessels are confined to the roots and have scalariform perforation plates with numerous bars. This type of vessel is also found in the roots of Tecophilaeaceae and Uvularieae (Colchicaceae–Uvulariaceae sensu Dahlgren et al., 1985).

Goldblatt et al. (1984) report raphide bundles in *Walleria mackenzii* Kirk and also in *Cyanella lutea* L. fil. of the Tecophilaeaceae, but not in *Cyanastrum cordifolium* Oliv. of Cyanastraceae.

Vegetative anatomy in *Walleria* was briefly described by Arroyo (1986).

Sterling (1974), in a study of genera of Liliaceae tribe Uvularieae, also included *Walleria.* He found small septal glands in *W. nutans* Kirk; in the other species studied, septal nectaries were lacking. He also observed fusion between ovary base and tepals often to a level above the locular base, and that raphide-containing idioblasts occur in the ovary wall. The bundles that are the source of ovular bundles seem to be fusion products of placental bundles and septal bundles.

Pollen morphology. The pollen grains of *Walleria* are heteropolar, sulcate, elliptic, 33 × ca. 23 μm large; polar axis ca. 20.5 μm long. Exine sculpture is irregularly rugulose. Tectum is densely and minutely perforate, on infratectal bacula. The sulcus is narrow and invaginated (J. Praglowski, unpubl. data; Fig. 20A).

Embryology and seed. According to Sterling (1974), the ovules are generally campylotropous, rarely anatropous, and are bitegmic and basitropic. The outer integument is several-layered, the inner two-layered. In "*W. armata,*" Sterling (1974) found that the nucellus is reduced to a small cap of tissue, whereas in the other species studied the nucellus is massive and free of the inner integument. A low obturator ridge at the base of the ovule was present (also known in Tecophilaeaceae, e.g., in *Odontostomum* Torr.). Details of embryo sac and endosperm formation are unknown.

Huber (1969) described the seed of *Walleria nutans.* It is elliptical, slightly curved (bean-shaped), and has a surface covered by warts or peglike projections arranged in rows and most

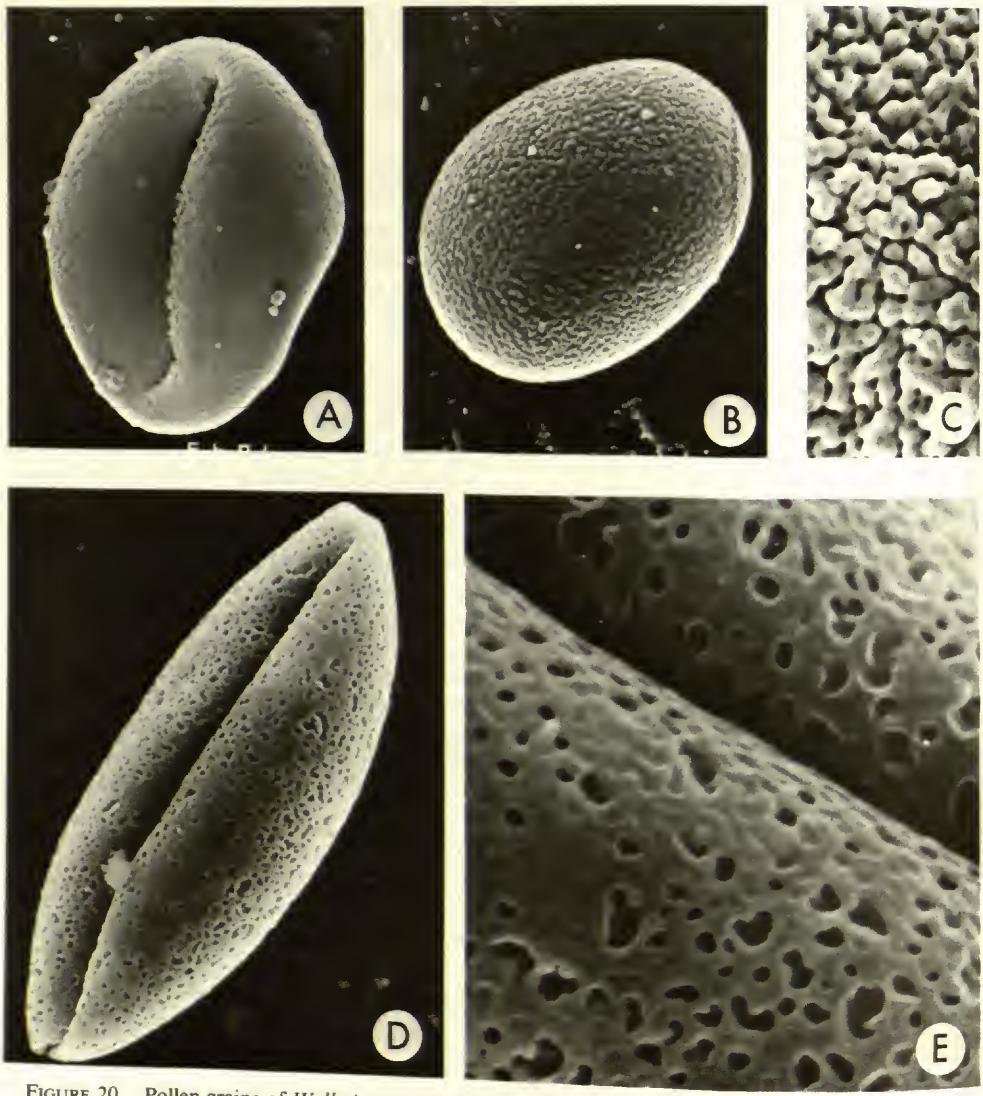


FIGURE 20. Pollen grains of *Walleria mackenzii* Kirk (Tecophilaeaceae subfam. Wallerioideae) (A–C) and *Eriospermum porphyrovalve* Bak. (Eriospermaceae) (D, E).—A, D. Pollen grains in distal views, showing the aperture.—B. Pollen grain, proximal view.—C. Detail of exine, proximal part.—E. Detail of exine along aperture. Magnifications: A, B. ×1,550; C. ×6,440; D. ×2,220; E. ×8,880. Material: A–C. *Strid 2538* (C); D, E. *O. J. Hansen 3221* (C). Preparation and photography by J. Praglowski (A–C) and Lu An-ming (D, E).

prominent on the chalazal end, where they are up to 0.5 mm high. Phytomelan is stated to be lacking by Huber (1969), but Carter (1966) described the seeds as dark red-brown and shiny (thus total absence of phytomelan in mature seeds requires verification). Each wart or peg bears an apical small fascicle of unicellular hairs, ca. 0.15 mm long. The epidermal cells of the wart apex, like other epidermal cells, are thick-walled and brownish, but part of each cell is exserted into a thin-walled, pale projection (= hair). The seed coat consists of 10–14 cell layers and is wholly made up of the outer integument, while the inner remains as a membrane of collapsed cells. The subepidermal cells of the seed coat are thick-walled and often filled with starch grains. The endosperm cells contain aleuron and fatty oils and have rather thick walls. Endosperm tissue

fills up most of the seed lumen. The embryo is large and cylindrical, slightly curved, and about two-thirds as long as the endosperm.

Chromosome number. Probably unknown.

Phytochemistry. Poorly known. Raphides are present in at least leaves and floral parts.

Conclusions and relationships. As outlined above, *Walleria* shows similarities both to Colchicaceae and Uvulariaceae of Liliales and to Tecophilaeaceae in Asparagales.

Arguments for an asparagalean affinity are (see Dahlgren et al., 1985: 131): 1) presence of raphides; 2) nonpatterned tepals without nectar grooves; 3) presence of septal nectar glands, though occasional and reduced; 4) pistil with a single, unbranched style and punctiform stigma; 5) crassinucellate ovules; 6) a seed coat with the inner integument (tegminal layer) compressed to a thin membrane.

Arguments for a lilialean affinity are: 1) the underground tubers; 2) the leafy stem with foliose leaves on distal parts; 3) the cirrhous leaf apices (typical of some genera in Colchicaceae); 4) the nonphytomelaniferous seeds.

Neutral are the basifixed anthers, the sulcate type pollen grains, and the introrse anthers.

The asparagalean features dominate, and some of the lilialean similarities are dubiously significant. Thus tuberous underground parts occur in both Eriospermaceae and Cyanastraceae, which (in spite of lacking a phytomelan layer) for various reasons are also considered members of Asparagales; a foliose inflorescence is found in other Asparagales, e.g., many Convallariaceae, and is also unusual in Liliales; and the non-phytomelaniferous seeds are undoubtedly connected with the warty, unusual surface structure, phytomelan lacking also in seeds in some other groups of Asparagales. The nature of the fruit, if originally fleshy, may be connected with the loss of phytomelan; usually, baccate-fruited Asparagales lack this pigment.

Further support for treating *Walleria* in Asparagales is its similarities to one particular group in this order, viz., Tecophilaeaceae, in which it has also been placed frequently in modern taxonomic literature. The similarities to Tecophilaeaceae include: 1) the erect leafy stem; 2) general similarity and color of perianth; 3) the tendency for basal fusion between perianth and ovary base; 4) the elongate poricidal anthers (similar, in particular, to those in *Conanthera* Ruiz & Pav.); 5) the narrow style with punctiform stigma; 6) the presence of an obturator ridge on the placenta; and 7) the multilayered testal part of the seed coat.

Conspicuous differences from Thecophilaeaceae sensu stricto are: 1) the lobate, untunicated tuber, on which roots are not restricted on the lower surface; 2) the foliose inflorescence; 3) the presence of hooks on stems and leaf midribs; 4) the cirrhous leaf apices; 5) the mostly campylotropous ovules; 6) the warty, nonphytomelaniferous (?) seed surface, with the small hair tufts crowning each wart; and 7) the relatively large, slightly curved embryo filling up two-thirds of the seed lumen.

The possible functional adaptations of the last-mentioned seed characters deserve particular study. It is possible, but not certain, that the poricidal anthers in *Walleria* have evolved independently of those in Tecophilaeaceae. The pollen grains of *Walleria* deserve further study as regards the apertural wall, but in general type agree with those in Tecophilaeaceae.

Similarities with Eriospermaceae (= *Eriospermum*), which likewise lack a phytomelan layer on the seed coat and have testal trichomes, are superficial. The details are widely different, and a close relationship is unlikely.

Also Cyanastraceae (= *Cyanastrum*) lack phytomelan on the seeds. They too show clear affinity to the Tecophilaeaceae in vegetative and floral features (e.g., poricidal anthers) but exhibit other specializations of the seed (a well-developed starchy chalazosperm, a large, globose embryo, lack of endosperm). This family may have evolved from an ancestral group that gave rise also to Tecophilaeaceae. Instability and disposition for evolutionary changes in the seed seem to be characteristic of this group.

On the basis of the above conclusions, *Walleria* is here included in Tecophilaeaceae of the Asparagales, but—on the basis of several important differences—is segregated as a separate subfamily, Wallerioideae.

Cyanastraceae Engler

Description. See, for example, Cronquist (1981) and Dahlgren et al. (1985).

General information. The family consists only of the genus *Cyanastrum* Oliv. with 4–7 species found mainly in forests of tropical Africa. Clausen (1940) recognized seven species, but Carter

(1962) reduced the number of species to only four.

Discussion. The family is discussed here only to the extent that it is of interest in connection with the families Tecophilaeaceae, Walleriaceae, and Eriospermaceae.

The tuber in *Cyanastrum* is not tunicated; it is often disc- or platelike, and constricted laterally. The roots emerge directly from the sides of the tuber. It is thus different from, but somewhat resembles, the tuber in *Walleria* (Tecophilaeaceae). Vessels are confined to the roots and have scalariform perforation plates, as in the Tecophilaeaceae.

The stem is erect and basally bears scale leaves (cataphylls), and one to three well-differentiated foliage leaves, which may be subsessile and oblanceolate (*Cyanastrum johnstonii* Bak.) or petiolate with a broad cordate-ovate lamina (*C. cordifolium* Oliv., *C. hostifolium* Engl.) with arching main veins connected by transverse veinlets. The aerial stem bears one or more sheathing bracts, these often large, and terminates in a raceme, which may be branched basally. The habit is quite different from that of Tecophilaeaceae and indicates secondary adaptation to tropical forest habitats, e.g., in the amplified leaf lamina.

Raphides are reported to be absent, but secretory spaces with oil-like secretion are present in the leaves. In this feature *Cyanastrum* seems to differ from Tecophilaeaceae. However, the presence of raphides in the leaves of *Cyanastrum* is implied in a recent paper by Arroyo (1986).

As in most Tecophilaeaceae, the flowers are half-epigynous and the tepals basally form a short floral tube, on the margin of which the six equal stamens are inserted. The anthers, as in Tecophilaeaceae, are poricidal. Microsporogenesis is simultaneous, and the pollen grains (Zavada, 1983) are sulcate (to trichotomosulcate) and tectate-columellate with a finely reticulate exine.

The ovary has three centrally situated septal nectary grooves (Nietsch, 1940, fig. 23). It is 3-lobed and 3-locular with two basal anatropous ovules in each locule. The central, simple style is gynobasic. As in Tecophilaeaceae (incl. *Walleria*), there is an obturator fold at the base of the ovules. The following embryological data by Nietsch (1940) are of interest. The ovules are anatropous, bitegmic, and weakly crassinucellate (a parietal cell is probably formed). The nucellar part is long and narrow. At the apex of the nucellus there is a nucellar cap formed in part through periclinal divisions of the epidermis. Embryo sac formation follows the *Polygonum* type. Cells at the chalazal end of the ovule divide and form an extensive nutrient tissue filling up about half of the seed, a chalazosperm, the cells of which contain fat and compound starch grains. The embryo, which fills up the remaining space (endosperm is virtually lacking), is subglobose and widely different from the embryo in all other Asparagales. The main part of it directly forms the tuber of the young plant.

Conclusions and relationships. Cyanastrum is unique in a number of features, including morphology, anatomy, and seed structure. It is clearly appropriate, therefore, to place the genus in its own family, Cyanastraceae.

In the unspecialized features, *Cyanastrum* agrees largely with the Tecophilaeaceae and should be placed in Asparagales next to this family (and also Lanariaceae). The specializations of the seed to some degree correspond to, but are clearly different from and independent of, those that have evolved in *Eriospermum* (= Eriospermaceae).

Eriospermaceae S. L. Endlicher

Description. Geophytic perennials with a hypocotyledonary tuber or a proliferation of tubers and stolons. Tubers generally globose, rarely elongate-cylindric, with opaque, white, yellow, pink or purple contents, growing point apical or lateral; slender rhizomes up to 10 cm long sometimes formed, securing vegetative propagation. Leaves either synanthous or heteranthous, rosulate, solitary or several, dorsiventral, variable in size, basally sheathing, linear or lanceolate (and sessile) to ovate or broadly cordate and then prostrate, if broad basally constricted into a narrow pseudopetiole, glabrous or pubescent; the base ultimately fibrous; veins parallel or arching, often connected by thin transverse veinlets; ca. 10 species, with complex, pubescent, more or less dissected enations from the upper part of the relatively small leaf blade; these resembling a group of feathers or a bottle brush or consisting of several threads. Inflorescence a simple scapose raceme, the scape subtended by a basal cataphyll, 3 to >100 flowered, borne in axils of membranous bracts. Flowers pedicellate, ebracteolate, bisexual, actinomorphic, hypogynous, trimerous, pentacyclic, often scented. Tepals free; the two whorls similar or dissimilar, white, pink or yel-

low, spreading or erect, often acute, when dimorphic the outer narrower and somewhat more spreading than the inner, these then often obovate and erect. Stamens 3+3, ± similar; filaments basally attached to the tepals, ± flat, broad and ovate or triangular to narrow and subfiliform; anthers dorsifixed, epipeltate, elongate, 2-thecate, 4-sporangiate, dehiscing longitudinally. Pollen grains dispersed singly. Pistil tricarpellary, with globose, ± lobate, 3-locular ovary and an erect, simple, filiform style, stigma simple, small, apical, papillate. Septal nectaries present. Ovules few to several, in two axial rows in each locule, anatropous. Fruit a smooth loculicidal capsule. Seeds comma-shaped, without phytomelan, covered with long, white or later rust-colored hairs.

General information. Eriospermaceae consist only of the genus *Eriospermum* Jacq., which consists of 80–100 species (Bond & Goldblatt, 1984; Perry, pers. comm.). The genus is confined to Africa south of the Sahara. Many species (ca. 30) are concentrated in the southwestern Cape Province.

Treatment in the literature. *Eriospermum* has generally been placed in Liliaceae sensu lato, but was recognized early (Baker, 1877) as a distinct tribe, Eriospermeae, on the basis of its peculiar habit, the larger tubers, and the seeds with long, silky hairs. Since then it has often been treated in a separate tribe or subtribe. It was generally placed in Liliaceae subfam. Asphodeloideae or tribe Asphodeleae, e.g., by Bentham & Hooker (1883) and Engler (1888). Melchior (1964) was representative in placing *Eriospermum* in Liliaceae subfam. Asphodeloideae tribe Bowieae. Airy Shaw (1973) treated it in Liliaceae tribe Asphodeleae subtribe Eriospermineae. The position of *Eriospermum* is not stated in any of the classifications of Takhtajan (1980), Cronquist (1981), or Thorne (1981, 1983), being supposedly included in Liliaceae. Lotsy (1911), who distinguished several natural groups of genera in the Liliiflorae as families, distinguished Eriospermaceae as a separate family, which he placed between Asphodelaceae-Aloëaceae and Johnsoniaceae. Huber (1969), drawing attention to the peculiar seed of *Eriospermum,* considered the genus distinct enough to be treated as a family of its own. This was partly necessitated by the breaking up of Liliaceae sensu lato into many segregate families distributed largely among two major groups: the "asparagoid Liliiflorae" (= Asparagales) and the "colchicoid Liliiflorae" (= Liliales). Eriospermaceae was later also recognized as distinct by Dahlgren (1980a), Dahlgren & Clifford (1982), Bond & Goldblatt (1984), and Dahlgren et al. (1985) as the unigeneric family suggested by Huber (1969). Archibald (1960) described several new species and gave interesting notes on correlation between color of tubers and dimorphic shape of tepals. New general information given by Perry (unpubl. data) and an embryological account by Lu (1985) further accentuate its advancement in several characters of ovule and seed. In Lu's work Eriospermaceae is upheld, but its relationships are still considered uncertain, although possibly closest to some Hyacinthaceae (e.g., *Bowiea* Harv. ex Hook. f.).

Gross morphology. Many details still remain to be studied in *Eriospermum.* Conventional studies generally do not prove sufficient due to 1) the short time of flowering, often only two to three weeks in late summer (when collecting activity is low); 2) the sporadic occurrence and dependence on rain for development; 3) the inconspicuous appearance of many species; 4) the fact that two or more species often grow mingled; 5) and that inflorescences are generally developed at a different time of the year than the leaves (see Archibald, 1960).

Duthie (1940), in a detailed account, described the genus *Eriospermum,* giving special attention to the unique enations from the leaf lamina found in some species. These, according to her, are important photosynthetic structures because their size is related to that of the leaf blade itself: the larger the enations the smaller the lamina. Their shape, as within *E. paradoxum* Ker-Gawl., is extremely variable (see Duthie, 1940: 55). Their morphological nature and the conditions under which they are formed may need further study, but they are not likely to contribute to solving the relationships of *Eriospermum.*

One interesting fact is that the species, in which the tubers have whitish or yellowish flesh, have subequal tepals, whereas the species that have tubers with reddish flesh also have dimorphic tepals, the outer tepals being narrower than the (often erect) inner ones. It is obvious that the genus can be divided into two (or more) species groups on the basis of these characteristics.

Anatomy. Little anatomical information is available for *Eriospermum.* According to a short note by Baijnath & Perry (1980), based on 11 species of the genus, stomata occur on both sides

of the leaves. There is no costal/intercostal zonation. The stomata are anomocytic and are either oriented parallel to or randomly in relation to the leaf axis, which is unusual in monocotyledons, but often associated with broad leaves. The epidermal cells vary in shape and are 2–20 times as long as they are wide. The hairs are distributed variably and their taxonomic value should not be overemphasized (Archibald, 1960). They are unicellular, and their base surrounded by a circle of epidermal cells (Baijnath & Perry, 1980). Archibald (1960) remarked that spots appearing on the leaf blades correspond to cells or groups of cells filled with mucilage.

Pollen morphology. The pollen grains of *Eriospermum porphyrovalve* Bak. (Fig. 20D, E) are fusiform ("boat-shaped"), ca. 45 × 17 μm, with a sulcus reaching along the whole length of the pollen grains. The exine surface is slightly foveolate and punctate, with rounded to lobate perforations variable in size, density, and distribution (voucher: *O. J. Hansen 3221*, C). In other species (e.g., *E. barerianum* Schinz; voucher *Seydel 3750*, C), the pollen grains are basically similar but proportionally somewhat broader, and with perforations more regularly dispersed and all more regularly circular.

The pollen type found in *Eriospermum* is common in the Asparagales.

Embryology and seed. The embryology was described by Lu (1985), whose data are as follows. The anther wall, as in most monocotyledons, consists of an epidermis, with flattened cells, an endothecium, a middle layer, and a single-layered, glandular tapetum containing cells with one or two nuclei. Microsporogenesis is successive, and most pollen tetrads when formed are isobilateral. The pollen grains are 2-celled when dispersed and have a small generative cell.

The ovules are anatropous and bitegmic. Papillose, palisadelike cells on the placenta adjacent to the micropyle of the ovules form an obturator (Lu, 1985, fig. 3B). Both integuments are largely 2-layered (the micropylar part of the inner integument 3-layered). The micropyle is formed by the inner integument. The archesporial cell cuts off a primary parietal cell, which remains undivided during meiosis; substantial parietal tissue is not formed. The nucellar epidermis does not divide periclinally either. Embryo sac formation is of the *Polygonum* type. The 8-nucleate embryo sac is situated immediately below and also borders laterally on the nucellar epidermis, while the nucellar tissue forms a column on the chalazal side of the embryo sac and a substantial tissue around this column. This divides later to enclose part of the embryo. Endosperm formation is nuclear, but the endosperm is poorly developed. The initial divisions of the embryo conform to the Solanad type, which is unusual in monocotyledons. The embryo develops rapidly and becomes cylindrical, straight, and almost as long as the seed lumen. The nucellar tissue mentioned above forms a sheath around the chalazal half or more of the embryo. The cells of this tissue are filled with oil drops.

The inner integument of the seed coat of the ripe seed is a thin film of compressed cells, a feature typical of asparagalean families (Huber, 1969); the outer integument consists of the epidermis and two more cell layers, which are compressed and colorless or contain a brown pigment ("phlobaphene") (Huber, 1969). The epidermal cells are each prolonged into a long, unicellular hair, which is initially whitish but becomes somewhat rust-colored with age. No phytomelan layer is developed.

Several of the above features are extraordinary in the Liliiflorae and indicate specialization and advancement: 1) the long testal indumentum; 2) the large embryo; 3) the lack of endosperm and, instead, presence of a nucellar tissue (actually a type of perisperm), the cells of which contain oil; and 3) the Solanad type of embryogeny.

Chromosome numbers. According to Perry (pers. comm.), Vosa has found the following chromosome numbers in *Eriospermum* species: $2n = 10, 12, 14, 20, 24$ and 42. The basic number appears to be $x = 7$.

Phytochemistry. Probably largely unknown.

Conclusions and relationships. Eriospermaceae are here considered best placed in the order Asparagales on the basis of the habit (rosulate leaves, scapose raceme), presence of septal nectaries, a pistil with a simple unbranched style, epipeltate anthers, and the seed coat with a collapsed inner integument. Lack of a phytomelaniferous layer is apparently connected with the development of indumentum from the testal epidermis. No other order can be seriously considered for housing Eriospermaceae.

Within Asparagales, the affinities of *Eriospermum* are less clear. It shares the tuberous underground parts with families such as Tecophilaeaceae–Wallerioideae, Cyanastraceae, and

Ixioliriaceae, all of which differ in having ± leafy stems, simultaneous microsporogenesis, and different seeds. The seeds in Tecophilaeaceae (except *Walleria* Oliv.) and Ixioliriaceae are phytomelaniferous; those in all Tecophilaeaceae and Cyanastraceae have a multilayered seed coat formed by the outer integument; those in all families except Cyanastraceae have copious endosperm; and those in Cyanastraceae have a peculiar chalazosperm, which is starchy and very unlike the perisperm in *Eriospermum*; all except Tecophilaeaceae subfam. Wallerioideae have glabrous seeds, and the hairs of the latter are very different from those in Eriospermaceae. The successive microsporogenesis and few-layered testa of *Eriospermum,* in particular, support the concept that this genus is not related to the above group of families. The occurrence in some species of *Eriospermum* of fascicled hairs in the inflorescence directs the attention to the Hypoxidaceae, which also have successive microsporogenesis and a few-layered testa. However, the Hypoxidaceae have amoeboid tapetum, helobial type of endosperm formation, and phytomelaniferous, endospermous seeds unlike those in *Eriospermum.*

The bulbous Hyacinthaceae, which otherwise agree with *Eriospermum* in the scapose racemose inflorescence, only rarely lack a phytomelan layer of the seeds, and these are endospermous with a smaller embryo. Differences of underground parts and in seed clearly distinguish *Eriospermum* from all Hyacinthaceae, although in *Bowiea* the embryo may become fairly large (*Eriospermum* and *Bowiea* have been associated earlier, but on rather loose grounds).

At present it is evident that *Eriospermum* is not only distinct enough to be treated in its own family, but that this family is clearly isolated in Asparagales and that no close relatives can be identified.

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THE PALMS OF AFRICA AND THEIR RELATIONSHIPS

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ABSTRACT

The palm flora of Africa is considered in the context of a new system of classification of the family (Dransfield & Uhl, 1986). Three subfamilies—Coryphoideae, Calamoideae, and Arecoideae—occur on the mainland of Africa. Coryphoideae are represented by six genera in three tribes, Calamoideae by five genera in one tribe, and Arecoideae by four genera in three tribes. The flora is certainly poor when compared with that of neighboring Madagascar or of the Asian or American tropics, and of the 15 genera only seven are endemic. However, the flora consists of such diverse and often peculiar and isolated elements as to argue for a much greater diversity and number of taxa in the past. In particular, Calamoideae in Africa include two of the most primitive and one of the most advanced genera, suggesting that the continent has been a major center of evolution for the subfamily. Possible narratives for the history of the African palm flora are discussed.

RÉSUMÉ

La flore des palmiers d'Afrique est ici considérée dans le contexte d'un nouveau système de classification de la famille (Dransfield et Uhl, 1986). Trois sous-familles (les Coryphoïdées, Calamoïdées et Arecoïdées) sont présentes sur le continent africain. Les Coryphoïdées sont représentées par six genres dans trois tribus, les Calamoïdées par cinq genres dans une tribu et les Arecoïdées par quatre genres dans trois tribus. La flore est assurément pauvre si on la compare à celle de Madagascar ou des tropiques asiatiques ou americaines. Sur les 15 genres, sept seulement sont endémiques. Cependant, la flore est composée d'éléments si divers et si souvent curieux et isolés que l'on peut témoigner en faveur d'un plus grand nombre et d'une diversité plus importante de taxons dans le passé. Les Calamoïdées africaines en particulier comprennent deux des genres les plus primitifs et l'un des plus avancés, ce qui suggère que le continent a été un centre d'évolution important pour la sous-famille. L'auteur mentionnera des explications possibles sur l'histoire de la flore des palmiers africains.

Palms are conspicuous components of several vegetation types in Africa and are of great economic significance both to subsistence cultures and to highly organized commercial agriculture. In Africa palms occur in perhaps greatest abundance in terms of species and individuals in the low-lying swamplands of the perhumid areas of West Africa (Letouzey, 1978); here *Raphia* and climbing palms predominate but *Phoenix* and other genera also occur. Further inland and in more seasonal climates *Phoenix* and *Elaeis* are present as conspicuous components especially in riparian forest. In savanna vegetation, species of *Hyphaene* and *Borassus aethiopum* grow in vast stands in some parts of the continent, though their distribution and abundance may be partly influenced by human activities. Finally, in deserts and subdesert steppes, *Hyphaene* and presumably the now almost extinct *Medemia* occur in oases and, together with cultivated or feral *Phoenix dactylifera,* are extremely important to human survival as sources of food, fuel, fodder, fiber and construction material.

Although palms are so important locally in the vegetation of Africa, it is well known that the total palm flora of the continent is poor (Table 1) in terms of both number of genera and species when compared with that of other parts of the tropics. Madagascar has an astonishingly rich and diverse palm flora consisting of about 120 species in 20 genera, of which 12 genera are endemic (Jumelle & Perrier, 1945, and additions). Yet the palm flora of the island is still poorly known; fragments of palms collected in Madagascar by a palm enthusiast from California suggest the presence of even greater diversity, indicating the great importance of the Madagascar palms in understanding the evolution of the family (Dransfield & Uhl, 1984). Further work on this unique palm flora is planned. The palm flora of the South American continent consists of about 837 species in 64 genera and that of the Eastern Tropics, admittedly a phytogeographically heterogeneous area, consists of 97 genera and about 1,385 species (Moore, 1973a). In one particularly rich area of the Sunda Shelf, an area of about only ten square kilometers carries a palm flora of 18 genera and 77 species (Dransfield, 1982). Although numbers of palms in America and Asia are in need of critical reassessment, the contrast

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TABLE 1. African palm genera with the total number of species and total species of endemics in mainland Africa.

	Total Number of Species	Number in Africa	Number of African Endemics
Chamaerops	1	1	0
Livistona	29	1	0
Phoenix	ca. 17	3	1
Borassus	ca. 6	1	1
Hyphaene	ca. 10	ca. 7	4
Medemia	1	1	1
Laccosperma	7	7	7
Eremospatha	12	12	12
Calamus	ca. 370	1	1
Raphia	28	28	26
Oncocalamus	5	5	5
Podococcus	1	1	1
Sclerosperma	3	3	3
Jubaeopsis	1	1	1
Elaeis	2	1	0[a]

[a] Possibly introduced in Madagascar.

between the 15 genera and 72 species in the whole of the mainland of Africa is very striking. I have excluded from the palm flora of the African mainland one endemic palm from Pemba Island, off the coast of Tanzania. *Chrysalidocarpus pembanus* H. E. Moore (Arecoideae: Areceae: Dypsidinae) is the only member of a genus of 20 species found outside Madagascar and the Comores. That it has not reached mainland Africa is remarkable, but in this it rather nicely parallels the genus of flying fox, *Pteropus,* which reaches Zanzibar but not the African mainland (Marshall, 1983). This coincidence of distributions may even be significant.

The most important recent analysis of the palm flora of Africa and its relationships is the paper of Moore (1973b) in which the palm floras of the forested regions of Africa and South America are analyzed and compared and the biogeography of the whole family discussed. Moore concludes that the palms probably had an origin in West Gondwanaland, whence they spread throughout the tropics and subtropics. It might be thought that the present paper would be superfluous in view of the thoroughness of Moore's paper. However, since the death of Hal Moore in 1980, I have been involved in completing and preparing for publication *Genera Palmarum,* together with Natalie Uhl of the Bailey Hortorium at Cornell University. Partly basing our work on the unpublished manuscript notes of Moore, we have critically reviewed generic limits and, with much new evidence available to us, have formalized a suprageneric classification of the family which we believe more clearly reflects relationships than the informal system published by Moore (1973a). The new classification does have considerable bearing on theories of the origin and dispersal of the family, and Africa, with its very limited but very peculiar palm flora, occupies a crucial position in such theories. What follows is largely the result of collaborative work with Natalie Uhl, but the phytogeographical speculation and shortcomings of the present paper are very much my own.

FOSSIL RECORD

The fossil record of palms in Africa is, not surprisingly, sparse, but there is evidence of a sudden development and increase in the presence of palmlike pollen in the Lower Senonian of West Africa (Jardiné & Magloire, 1963; Muller, 1979), suggesting at least a long presence of the family in Africa. Pollen of *Nypa,* at present confined to Southeast Asia, Malesia, and the Pacific, has been reported from the Maestrichtian of Cameroon, and pollen referred to *Areca ipot* has been reported from the same time and area (Muller, 1981). Pollen referred to *Elaeis* and *Sclerosperma* has been reported from the Miocene of West Africa. Megafossils are rare. The significance of the fossil pollen will be discussed below.

THE PALM FLORA OF AFRICA

The new suprageneric classification of the palms (Table 2) indicates the systematic position of the African representatives of the family.

CORYPHOIDEAE

The subfamily comprises three tribes. Tribe Corypheae consists of 31 genera arranged in four subtribes. There are two representatives in Africa. *Chamaerops,* a monotypic genus in the primitive subtribe Thrinacinae, is present on the Mediterranean coast of north Africa; elsewhere it is found in southern Europe. Its closest relatives are *Rhapidophyllum* (1 sp.) in the southeastern U.S.A., and *Trachycarpus* in China and the Himalayas. The other members of the subtribe are distributed in China and Southeast Asia (3 genera) and Central and South America and

the Caribbean (8 genera). *Chamaerops* seems to represent a relic of a Madrean-Tethyan flora.

Livistona in Africa is represented by a single species, *L. carinensis* (Chiov.) J. Dransf. & N. Uhl, formerly regarded as belonging to a monotypic genus, *Wissmannia* (Dransfield & Uhl, 1983). The species is also found in Arabia. The genus belongs to subtribe Livistoninae and consists of about 28 species, with the exception of *L. carinensis,* distributed from India to Southeast Asia, Malesia and, especially, Australia. The subtribe is largely Northern Hemisphere in distribution, occurring abundantly in both New and Old Worlds and the Pacific. Its absence from Africa (apart from *L. carinensis*) and Madagascar is noteworthy. This subtribe contains several genera that are moderately to strongly drought resistent. That there is only one member in Africa, and that it is a nonendemic species of a largely Asian or Malesian genus, suggests it may be a relatively recent immigrant from the Asian region and further suggests strongly, at least to me, that the subtribe may never have had a greater representation on the African continent. The subtribe is also absent from much of South America (except for the widely dispersed species of the otherwise Caribbean genus *Copernicia*).

Tribe Phoeniceae consists of the single genus *Phoenix*. Despite the great economic importance of several of its species, in particular the date *P. dactylifera* L., the taxonomy of the genus is very poorly understood. There are about 17 species; of these *P. reclinata* Jacq. is apparently endemic to Africa, and *P. caespitosa* Chiov. is present in northeastern Africa and Arabia. The date palm is widely cultivated in the drier areas. *Phoenix* has a distribution ranging from the Atlantic islands of Cape Verde and the Canaries to the Indian subcontinent, China, Southeast Asia and the Philippines. Greatest morphological diversity occurs in India. One species, *P. theophrastii* Greuter, is present in Crete and the Mediterranean coast of Turkey. The generic identity of the fossils attributed to *Phoenix* cannot always be relied upon. Fossil fruits have been recorded from the late Eocene or Oligocene of Texas and pollen from the Eocene London Clay. *Phoenix* does appear to have a largely Laurasian or Tethyan distribution pattern, apart from the widespread African *P. reclinata*.

Tribe Borasseae, in marked contrast to the two other Coryphoid tribes, has a distribution centered on the lands adjoining the Indian Ocean and its islands. There are two subtribes, Lataniinae with four genera and Hyphaeninae with three. Of the former subtribe, the only African representative is *Borassus* with a single endemic species, *B. aethiopum* Mart. Hyphaeninae is represented by *Hyphaene,* a typically African genus, and *Medemia,* the single species *M. argun* (Mart.) Wuertt. ex H. A. Wendl. being on the verge of extinction (if not already extinct) in the Sudan and Egypt. *Hyphaene* has been greatly overdescribed but probably has only ten species, of which seven occur in Africa, four of them endemic. Elsewhere the genus occurs in Arabia, the Indian subcontinent, and possibly Sri Lanka. The greatest number of species and morphological diversity is in Africa. The only other genus in the subtribe, *Bismarckia,* has a single species endemic to Madagascar.

There are no fossils reliably referable to members of the tribe Borasseae. The present distribution (Africa, India, Southeast Asia, Malesia, Mascarene Islands, Seychelles, and Madagascar) suggests an origin of the tribe in Gondwanaland, followed by rafting on Gondwanalandic fragments, followed by limited dispersal.

CALAMOIDEAE

The Calamoideae ("Lepidocaryoid Major Group" of Moore, 1973a) comprises 22 genera. The subfamily has been divided into two tribes. Lepidocaryeae, with three genera, is confined to South America; its relationships with the rest of the subfamily are not obvious but may be with Asiatic genera rather than African. Tribe Calameae has been divided into eight subtribes. The basis for the division is primarily the arrangement of flowers in the inflorescence. Four of the eight subtribes are represented in Africa, and the African members of the subfamily include some of the most remarkable of all African palms. The basic arrangement of flowers in the subfamily is a dyad; all members of the subfamily except for *Oncocalamus* have flower groupings displaying some evidence of probable derivation from a dyad of flowers. The simplest condition in the subfamily is a dyad of hermaphrodite flowers. Only two genera display this simple, probably ancestral arrangement, viz *Laccosperma* (syn. *Ancistrophyllum*) and *Eremospatha*. Both of them are African endemics and have been separated as a distinct subtribe, Ancistrophyllinae. Of the two, *Laccosperma* has less specialized dyad structure in possessing clearly defined bracts and bracteoles; *Eremospatha,* on the other hand, is

TABLE 2. Suprageneric classification of palms including the African genera by name. Detailed distribution of African genera is outlined in Table 1.

CORYPHOIDEAE	
Corypheae	
Thrinacinae	14 genera, including *Chamaerops* in Africa
Livistoninae	12 genera, including *Livistona* with one species in Africa
Coryphinae	4 genera
Sabalinae	1 genus
Phoeniceae	1 genus, *Phoenix*, represented by 2–3 species in Africa
Borasseae	
Lataniinae	4 genera, including *Borassus* with 1 species in Africa
Hyphaeninae	3 genera, *Hyphaene* and *Medemia* in Africa
CALAMOIDEAE	
Calameae	
Ancistrophyllinae	2 genera, *Laccosperma* and *Eremospatha*, both endemic to Africa
Eugeissoninae	1 genus
Metroxylinae	2 genera
Calaminae	8 genera, 1 species of *Calamus* in Africa
Plectocomiinae	3 genera
Pigafettinae	1 genus
Raphiinae	1 genus, *Raphia*, predominantly African
Oncocalaminae	1 genus, *Oncocalamus*, endemic to Africa
Lepidocaryeae	3 genera
NYPOIDEAE	1 genus, introduction in W. Africa
CEROXYLOIDEAE	
Cyclospatheae	1 genus
Ceroxyleae	5 genera
Hyophorbeae	5 genera
ARECOIDEAE	
Caryoteae	3 genera
Iriarteeae	
Iriarteinae	4 genera
Wettiniinae	2 genera
Podococceae	1 genus, *Podococcus*, endemic to W. Africa
Areceae	
Oraniinae	2 genera
Manicariinae	1 genus
Leopoldiniinae	1 genus
Malortieinae	1 genus
Dypsidinae	6 genera
Enterpeinae	6 genera
Roystoneinae	1 genus
Archontophoenicinae	7 genera
Cyrtostachydinae	1 genus
Linospadicinae	4 genera
Ptychospermatinae	9 genera
Arecinae	8 genera
Iguanurinae	27 genera
Oncospermatinae	8 genera
Sclerospermatinae	2 genera, *Scerlosperma* endemic to Africa

TABLE 2. Continued.

Cocoeae	
Beccariophoenicinae	1 genus
Butiinae	9 genera, *Jubaeopsis* endemic to Africa
Attaleinae	4 genera
Elaeidinae	2 genera, *Elaeis* with 1 species in Africa
Bactridinae	6 genera
Geonomeae	6 genera
PHYTELEPHANTOIDEAE	3 genera

remarkable for the great reduction or almost complete absence of bracts in the inflorescence. Members of these two extraordinary genera are climbing palms or rattans, very similar in habit to the Asiatic rattans belonging to the Calaminae, Plectocomiinae and Metroxylinae. A third African genus, *Oncocalamus,* is almost indistinguishable from *Eremospatha* and *Laccosperma* in vegetative characters but it has an anomalous flower arrangement very difficult to interpret and compare with other members of the Calamoideae. *Oncocalamus* is monoecious and flowers of both sexes are found in the same flower cluster; the central one to three flowers are pistillate while the staminate flowers are arranged in two lateral cincinni, one on each side of the pistillate flowers, the whole cluster enclosed by a prophyll and the rachilla bract. The arrangement of bracts and bracteoles makes it difficult to imagine how this unique arrangement could have been derived from a dyad. Despite the extraordinary vegetative similarities, we have separated *Oncocalamus* from the Ancistrophyllinae into a subtribe of its own, Oncocalaminae. This must be regarded as one of the most advanced and peculiar subtribes in the Calamoideae.

The other manifestly African subtribe of the Calamoideae is the Raphiinae with the single genus *Raphia.* Like *Oncocalamus, Raphia* is monoecious. There are about 28 species, of which 26 are endemic to Africa. One species, *R. farinifera* (Gaertn.) Hyl. is also found in Madagascar where it is possibly introduced, and the other nonendemic species, *R. taedigera* Mart., long considered to be endemic to South and Central America, has recently been reported to occur in Africa (Otedoh, 1977). Unfortunately Otedoh's complete monograph of *Raphia* has yet to be published, so the full evidence cannot be assessed. However, Otedoh also shows how closely related *R. taedigera* is to *R. vinifera* P. de Beauv. and goes on to suggest that far from having reached the American continent by natural long-distance dispersal or having rafted on the South American plate when Gondwanaland broke up, *R. taedigera* was introduced to the New World about 400 years ago during the early days of the slave trade. If Otedoh's explanation of the presence of *Raphia* in the Americas is correct and *R. taedigera* was introduced, then its dominance in lowland swamps, especially in Costa Rica (Myers, 1984) suggests extreme success in colonization and suppression of native vegetation. Whatever the origin of *Raphia* in the Americas, it is nevertheless overwhelmingly an African palm genus, one of great interest and local importance. Unlike the other African members of the subfamily, species of *Raphia* are not slender climbers but, instead, are medium-sized to very robust acaulescent to tree palms with immense leaves, including the longest leaves ever recorded in the plant kingdom (Hallé, 1977). *Raphia* is distinctive in bearing single flowers in each rachilla bract, the basal bracts subtending pistillate flowers, the distal staminate. Very rarely at the junction of pistillate and staminate portions of the rachilla, one bract may subtend a dyad of a pistillate and a staminate flower. The bract number and arrangement seem to suggest derivation from a dyadic condition. Although obviously a member of the Calamoideae, *Raphia* is nevertheless an isolated genus without close relatives.

The fourth subtribe represented in Africa is the Calaminae itself, one genus, *Calamus,* occurring in the perhumid areas of equatorial Africa. African *Calamus* is variously regarded as being represented by ten closely related species or one very variable species. At present there is insufficient material and information of natural history to justify maintaining ten species. The genus is otherwise confined to Asia and Malesia. Despite being a climbing palm, it is very different

from *Laccosperma, Eremospatha* and *Oncocalamus.* Not only is the structure of the flower cluster totally different and the plants dioecious, but the climbing organs in the African species of *Calamus* are flagella, whiplike sterile inflorescences, rather than cirri, extensions of the leaf rachises bearing reflexed, modified, spinelike leaflets, found in the three endemic genera. *Calamus,* with well over 370 species, is the largest palm genus, and it is tempting to suppose that the African species is (or are) a relatively recent immigrant from India or Asia. A phylogenetic analysis of the genus might give supporting evidence but this is not yet practicable.

Overwhelmingly Calamoideae are an Asian or Malesian group. The greatest number of genera and species are to be found on the Sunda Shelf lands of Sumatra, Malaya and Borneo; the further away from this center, the fewer are the genera and species (Dransfield, 1981). Madagascar, which has a rich and diverse palm flora, does not possess any representative of the group apart from *Raphia farinifera,* which could, as suggested above, be introduced. Despite the dangers of arguing from absences, I am tempted to suggest that the Calamoideae have never been present on the Great Island and that they arose in a position too far from Madagascar to have been able to reach the island or at a time after the island had become separated from Africa. Yet the presence of the least specialized and some of the most advanced members of the subfamily in Africa does seem to suggest that the subfamily may have arisen on the land destined to become Africa and then have become dispersed along the shores of Tethys to Southeast Asia. The origin of the tribe Lepidocaryeae is perhaps the greatest problem. A phylogenetic analysis of the subfamily is in progress; when the results of this are available, it may be possible to speculate further.

ARECOIDEAE

The four remaining African palm genera belong to the Arecoideae. Arecoideae, in its latest sense (Dransfield & Uhl, 1986), includes several major groups or formal categories previously kept separate at the subfamilial level, all palms in which the basic flower arrangement consists of a triad of a central pistillate and two lateral staminate flowers or of an arrangement manifestly derived from a triad belong to the Arecoideae. Thus we have included in this subfamily the Caryotoid, Iriarteoid, Podococcoid, Cocosoid, Arecoid and Geonomoid, major groups of Moore (1973a), all as tribes of the one subfamily. The inclusion of the Caryotoid palms in the Arecoideae may appear heterodox in view of the induplicate rather than reduplicate vernation of the leaves. However, I have recently shown much greater variation in leaf vernation within Coryphoideae, suggesting that vernation may not necessarily be of such fundamental significance as thought previously (Dransfield, 1977; Dransfield et al., 1985).

Podococcus barteri G. Mann & H. A. Wendl. is the sole member of tribe Podococceae; this is a curious forest undergrowth palmlet confined to the humid tropical rain forests of West Africa. It is very isolated morphologically and its relationships are obscure. There are tantalizing parallels in morphology with the Iriarteeae of South America, but although there are similarities in leaf, flowers and fruit, there are striking distinctions related to the presence of pits in the rachillae of *Podococcus.* If the Iriarteae and Podococceae are more closely related to each other than to the other tribes, then they still probably diverged from each other long ago, probably at the breakup of Gondwanaland. I do not believe that *Podococcus* can be regarded as a member of the Iriarteeae.

Sclerosperma, with one or three very closely related species, is also a palm of the undergrowth of tropical rain forest. It is included in Areceae by virtue of the single peduncular bract that accompanies the inflorescence prophyll and the pseudomonomerous gynoecium. However, its position within the tribe is obscure. We have included it, together with *Marojejya,* a genus of two species from northeastern Madagascar, in a separate subtribe, the Sclerospermatinae, but this subtribe may not be monophyletic. Careful work on the Madagascar palms may eventually indicate the true relationships of *Marojejya. Sclerosperma* remains an extraordinary, isolated palm.

Tribe Cocoeae consists of 22 genera arranged in five subtribes. Apart from *Cocos, Jubaeopsis, Beccariophoenix* and one of the two species of *Elaeis,* all extant members of the tribe occur in the New World. A recently extinct member of the tribe occurred until perhaps 800 years ago on Easter Island in the Pacific Ocean (Dransfield et al., 1984). The natural distribution of *Cocos* has recently been shown probably to be in the West Pacific (Gruezo & Harries, 1984; Buckley & Harries, 1984). *Beccariophoenix* is confined to Madagascar, where a second member of the tribe

may also occur. The two remaining genera are African. *Jubaeopsis* is confined to one very small area of the Transkei in southern Africa, where it occurs on the rocky banks of a few estuaries. We have included the genus in the same subtribe as *Cocos, Butia, Jubaea, Syagrus, Lytocaryum, Parajubaea, Allagoptera* and *Polyandrococos.* Apart from the coconut, possibilities for long-distance dispersal in this group seem very limited and the presence of *Jubaeopsis* in southern Africa seems to argue for a very long presence of the subtribe on the African continent, of which *Jubaeopsis* is the only extant relic.

Elaeis is included with *Barcella* in a separate subtribe of the Cocoeae, Elaeidinae. Although clearly members of the tribe Cocoeae, the two genera of Elaeidinae are distinct in the fibrous peduncular bract, the lack of epidermal spines (as opposed to fiber spines), the pistillate flowers sunken in the rachillae, and the endocarp pores at or above the middle of the endocarp. *Barcella* continues to be very poorly known but what material is available suggests that, in terms of sexuality of the inflorescences and structure of the androecium, *Barcella* is less specialized than *Elaeis.* The two genera are, however, very closely related. *Barcella,* with one species, is confined to a small area of the Rio Padauiri in Brazil. *Elaeis oleifera* (H.B.K.) Cortes, on the other hand, is more widespread, occurring in both northern South America and Central America. There is a fossil pollen record referable to *Elaeis guineensis* Jacq. in the Niger delta back to the Miocene (Zeven, 1964) indicating the presence of the genus in Africa for a considerable period. However, in view of the relationships of the subtribe with other members of the Cocoeae, an American origin of the Elaeidinae seems more plausible than one in Africa. We may postulate dispersal of the ancestor of *E. guineensis* to Africa at latest by the end of the Oligocene.

The Origin of the African Palm Flora

It seems possible to separate the subtribes, tribes, or even subfamilies of the Palmae into those taxa which are predominantly Laurasian in distribution and those which are predominantly Gondwanic. There are exceptions in some of the taxa which may reflect poor taxonomy or which can be explained by relatively recent long-distance dispersal. However, some broad general patterns seem to me to be discernible. The following taxa are largely Laurasian: tribe Corypheae (with a few exceptions), tribe Phoeniceae, tribe Calameae (with a few exceptions), subfamily Nypoideae, and tribe Caryoteae. In contrast, the following are largely Gondwanic: tribes Borasseae, Lepidocaryeae, subfamilies Ceroxyloideae, Phytelephantoideae, and Arecoideae except Caryoteae and a few members of subtribes Arecinae and Iguanurinae of Areceae. Of particular note is that the three higher taxa containing apocarpous members are largely (but not entirely) Laurasian, and there seems good evidence for regarding syncarpy as being derived in the family (Moore & Uhl, 1982). The three higher taxa are subfamily Nypoideae with the single monotypic genus *Nypa,* tribe Phoeniceae with the single genus *Phoenix,* and subtribe Thrinacinae, one of the four subtribes of tribe Corypheae. Thrinacinae, however, is where the most important exceptions to the Laurasian bias occur.

Thrinacinae comprises 14 genera, all apocarpous. *Trithrinax, Chelyocarpus* and *Itaya* occur in South America and Central America, and *Schippia, Thrinax, Coccothrinax,* and *Zombia* occur in the lands adjacent to and the islands of the Caribbean. The remaining six genera are scattered through the temperate and subtropical regions of the northern hemisphere: *Rhapidophyllum* with one species in southeastern U.S.A.; *Chamaerops* with one species in north Africa and Europe; *Trachycarpus* with about five species in the Himalayas, Burma, northern Thailand and China; *Guihaia* with two species in China and Vietnam; *Rhapis* with about twelve species in China and Indochina; and *Maxburretia* with three species in Thailand and Malaya. Moore (1973b) stated that the distribution of these primitive apocarpic members of the Corypheae suggests an origin of the group in West Gondwanaland, followed by dispersal into North America, Europe, and East Asia. Implicit was the basal primitive position of the Corypheae within the whole family; thus the palms as a whole were postulated as having arisen in West Gondwanaland.

However, I suggest that the distribution of all the apocarpic palms might more economically be read in the other direction. I suggest it is worth considering a Laurasian origin of the family, followed by invasion into Gondwanaland very early in the history of their radiation, and evolution somewhat independently, some groups being much influenced by the breakup of Gondwanaland and presenting today a widely disjunct distribution in the southern hemisphere. The abun-

dance of simple, monocotyledonous-type pollen in the Potomac beds of the U.S.A. suggested to Walker (pers. comm.) the possibility that the monocotyledons may be Laurasian rather than Gondwanic in origin, and viewed in the context of this speculative idea, palms may indeed be more economically explained in terms of a Laurasian origin. The first, indisputable palm pollen is upper Cretaceous in age (Muller, 1981), but it must be remembered that pollen of Corypheae is of an unspecialized monosulcate type, indistinguishable from many other monocotyledonous families. It would thus be surprising if the first palms could be recognized as such from their pollen, and conversely, some of the earliest pollen grains referred to monocotyledons could be pollen of early palms.

Africa may well have been an important dispersal route for early palms, but at the present day the palm flora of the continent seems to consist mostly of obvious immigrants such as *Calamus* and *Livistona* and ancient, isolated relics such as *Sclerosperma* and *Podococcus. Raphia, Laccosperma, Eremospatha* and *Oncocalamus* display such morphological diversity as to suggest a long history and previously much more diverse representation of the subfamily. Indeed it may be suggested that Africa could have been the center of origin of this subfamily, whence it has spread and diversified in Southeast Asia, with one very problematic group of relatives in South America. The members of tribe Areceae also suggest a much more diverse flora in the past. In relation to this, mention must be made of the presence of fossil pollen in the Upper Cretaceous of Cameroon. *Retimonocolpites pluribaculatis* Salard-Cheboldaeff from the Maestrichtian of Cameroon has been equated with *Areca,* specifically with the pollen type found in *A. ipot* Becc., a very local endemic of the Philippines (Muller, 1981). In view of the extraordinary parallels in pollen form in the family (Ferguson, 1987) and the very limited distribution of *A. ipot,* I believe great caution should be shown in accepting the fossil pollen as belonging to *A. ipot* or even a near relative. From a phytogeographical point of view the presence of the highly advanced east Asiatic genus *Areca* in the Upper Cretaceous of West Africa would be hard to explain. On the other hand, if the grain does indeed represent a palm, then it does argue for early diversity of the family in Africa.

Conclusion

In conclusion, the curiously diverse but sparse palm flora of Africa, in my opinion, argues strongly for past diversity and widespread extinction. The great and well-known climatic vicissitudes (Moreau, 1952, 1963, 1966) of the past in Africa must surely have had a profound effect on the palms, causing serious depletion of taxa adapted to humid tropical environments, while others, such as the Borasseae, adapted to more arid conditions may actually have been favored and survive today with a relatively rich representation. It is possible that we may understand much more about the origins and dispersal of the family after the completion of a cladistic analysis already in its preliminary phases (Dransfield et al., in prep.).

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AFFINITIES OF THE AFRICAN DENDROFLORA: SUGGESTIONS FROM KARYO- AND CHEMOSYSTEMATICS[1]

FRIEDRICH EHRENDORFER[2]

ABSTRACT

Examples are presented from current comparative morphological, palynological, karyological, and phytochemical studies on tropical woody angiosperm groups among Annonaceae, Winteraceae, Laurales, Rutaceae, Dilleniaceae, Cochlospermaceae and Rubiaceae. The intention is to contribute to the understanding of the problem of the origins and intercontinental affinities of the African dendroflora from the reconstruction of phylogenetic connections and major migration routes. Many cases of relatively recent to remote or quite ancient affinities are illustrated, which link extant African groups with others in the Americas, the Malagasy region, Asia and Australasia, etc. In contrast, several instances of assumed intercontinental affinities are revealed as spurious, being based on "artificial" taxonomic grouping.

RÉSUMÉ

L'auteur présente des exemples tirés d'études actuelles comparatives morphologiques, palynologiques, karyologiques, et phytochimiques sur des d'angiospermes ligneux tropicaux parmi les Annonacées, Monimiacées, Winteracées, Dilleniacées, Flacourtiacées, Cochlospermacées, Rutacées, et Rubiacées. Le but est de démontrer des affinités inter-continentales de la dendroflore africaine à partir de la reconstruction de rapports phylogéniques et des routes majeures de migration. De nombreux cas d'affinités relativement récentes à anciennes sont illustrés. Ils relient des groupes africains existants à d'autres groupes sur le continent américain, à Madagascar, en Inde, dans l'Asie du sud-est, en Australie, dans le Pacifique ouest, etc. Contrairement, plusieurs exemples d'affinités inter-continentales présumées apparaissent fausses, étant basées sur un regroupement taxonomique artificiel.

One of the major lines of research at the Institute of Botany and the Botanical Garden of the University of Vienna (Austria) is the inquiry into the differentiation patterns and evolutionary processes of tropical woody angiosperms. Our approach is a synthetic one, utilizing information from comparative morphology and anatomy, palynology, karyology, phytochemistry, ecology, phytogeography, paleobotany, etc. I have selected several examples from our tropical research projects that have a bearing on the intercontinental relationships and phytogeographical links of the African dendroflora.

ANNONACEAE

The ancient and large pantropical family of Annonaceae comprises about 130 genera and more than 2,000 species. Comparative palynological analyses (e.g., LM: Walker, 1971a, 1971b, 1972; EM: Le Thomas, 1980, 1981; Hesse et al., 1985; etc.), karyological studies (e.g., Ehrendorfer et al., 1968; Tanaka & Okada, 1972; Okada & Ueda, 1984; Sauer & Ehrendorfer, 1984; Morawetz, 1986; etc.) and an increasing number of phytochemical data (e.g., Leboeuf et al., 1982, etc.) have shown that the available formal systematic arrangements of the Annonaceae (e.g., Sinclair, 1955; Fries, 1959; Hutchinson, 1964; Verdcourt, 1971) are often "artificial" and do not reflect phylogenetic relationships. Hopefully, our current efforts will improve this situation and thus will afford a more suitable basis for phytogeographical conclusions. The following examples illustrate this for African-American and African-Asian relationships among Annonaceae, ranging from the level of species to that of sections, genera, and tribes.

With ca. 120 species, ***Annona*** is one of the largest and morpho-ecologically most diverse genera in the family. Its pollen is mostly in tetrads, lacks distal apertures and has a columellate exine. Thus, according to Walker (1971a), it belongs to the *Annona* subfamily and the predom-

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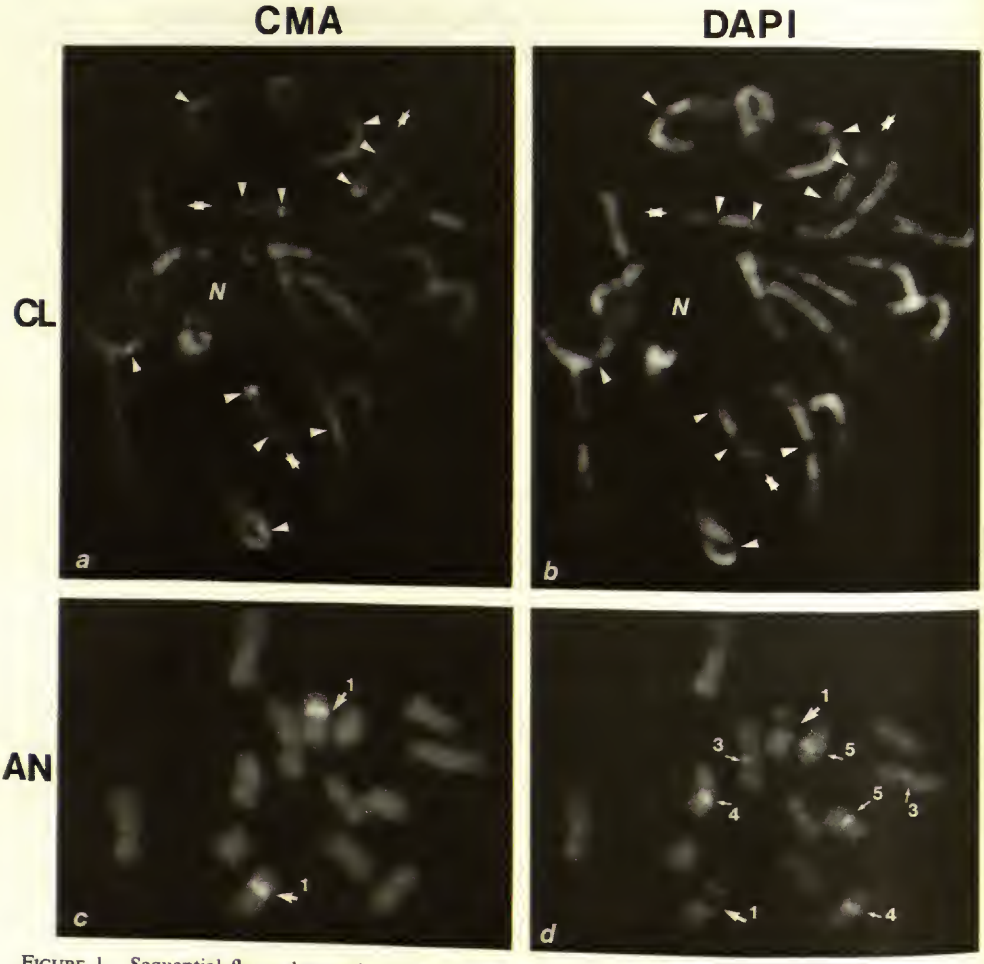

FIGURE 1. Sequential fluorochrome banding of prometaphasic endosperm chromosomes of *Cleistopholis patens* (CL, a, b, $3n = 21$) and metaphasic chromosomes of *Annona muricata* (AN, c, d, $2n = 14$) with the fluorochrome stains chromomycin A (= CMA): a, c and DAPI: b, d. Note the differences between the two taxa: *Cleistopholis* with three NO-chromosomes attached to the nucleolus (N) and with many, often CMA positive and DAPI negative, proximal, terminal and intercalary bands in the other chromosomes (a, b: short arrows), particularly well seen in the three probably homologous chromosomes marked by asterisks. *Annona* with two bright CMA positive (and DAPI negative) bands in the NO-chromosomes number 1 only (c, d: big arrows) and with DAPI positive bands in chromosomes numbers 3, 4, and 5 (d: small arrows). (Original from W. Morawetz.)

inantly neotropical *Annona* tribe, together with the clearly related *Raimondia, Rollinia* and *Rolliniopsis,* and the more remote African *Anonidium.* Among diploid species of *Annona* with $2n = 14$ ($x = 7$), there is only little karyotype differentiation (e.g., in respect to size of chromosomes, arm ratios and condensing patterns: Tanaka & Okada, 1972; Morawetz, 1984a, 1984b). After sequential DAPI and CMA staining, even species from very different sections exhibit the same fluorochrome banding pattern which is unique within the family (Morawetz, 1986, and Fig. 1): NO-chromosomes (pair 1) with a conspicuous $DAPI^-$ (negative)/CMA^{+++} (strongly positive) band, chromosome pairs 3 and 5 with a band $DAPI^{+++}/CMA^+$, chromosome pair 4 with a band $DAPI^{+++}/CMA^-$.

In addition, several species of *Annona* have become polyploid, with $2n = 28$ ($4x$), and $2n = 42$ ($6x$). *Annona glabra* is $4x$, morphologically rather uniform, and the only species of Annonaceae native to both the Neotropics and Paleo-

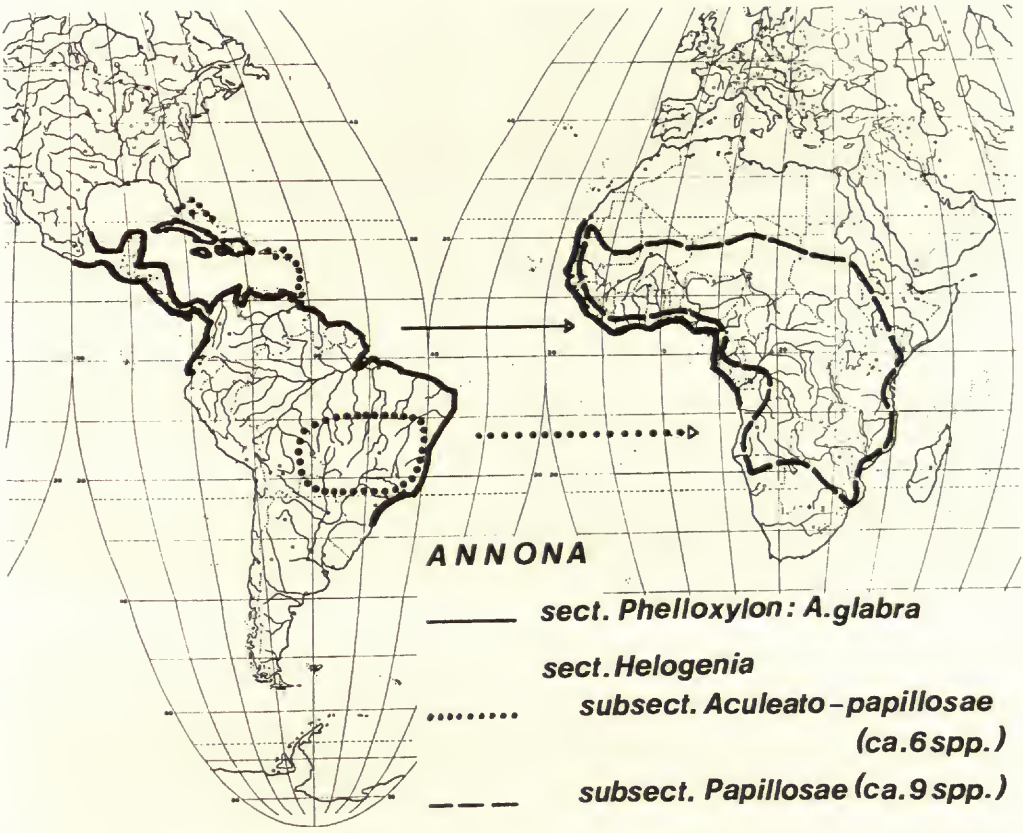

FIGURE 2. General distribution and suggested transatlantic migration routes of *Annona* sect. *Phelloxylon* (only *A. glabra*) and sect. *Helogenia* (ca. 15 neo- and paleotropical species).

tropics (W. Africa) (Fig. 2). It is the only member of the monotypic sect. *Phelloxylon* (Fries, 1959) distantly related to sect. *Psammogenia* in eastern South America (with the 2*x* rain forest species *A. salzmannii*, etc.). Diploidisation of the *A. glabra* karyotype is apparent from a change in the fluorochrome banding which has become completely DAPI and CMA neutral, in contrast to all other diploids studied (Morawetz, 1986). Otherwise, its chromosome sets have not diverged much (Thakur & Singh, 1969) and there are still two pairs of active NO-chromosomes (while other 4*x* have changed to one NO-pair only: Morawetz, 1984b). Thus, *A. glabra* can be ranked as a "mesopolyploid" without closely related diploid 2*x* relatives (Ehrendorfer, 1980; Sauer & Ehrendorfer, 1984), which must have achieved its transatlantic distribution by long-distance dispersal from tropical America to West Africa in the not-too-distant past.

Another example of a neo/paleotropic disjunction is represented within *Annona* by the clearly related savanna taxa of sect. *Helogenia* (Fig. 2), with subsect. *Aculeato-papillosae* in eastern Brazil (ca. 6 species) and subsect. *Papillosae* in tropical Africa (ca. 9 species) (Robyns & Ghesquière, 1934; Fries, 1959). It is quite obvious that the more advanced differentiation of these two subsections must be older than the transatlantic establishment of the rather uniform *A. glabra*.

An even more remote separation has to be assumed in regard to the predominantly American members of the ***Annona* tribe** ($x = 7$) and the genus *Anonidium*, with 4–5 species, mostly in western tropical Africa. The relationships of these two groups has been ascertained by recent morphological and palynological findings (Le Thomas, 1969, 1980, 1981), but affirmative karyological data are still lacking for *Anonidium* (there is the possibility of fairly close affinities of this genus with the African *Hexalobus* tribe,

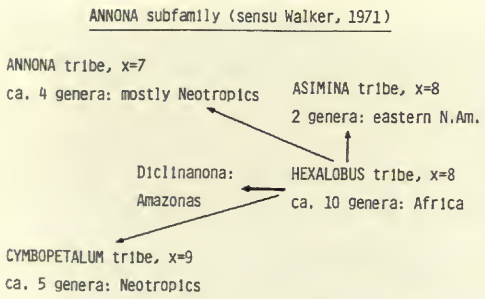

FIGURE 3. Affinities within the *Annona* subfamily (sensu Walker, 1971a) based on acknowledged trends in morphology, pollen structure, and chromosome base number.

characterized by $x = 8$). On the other hand, we can exclude any closer relationships between *Annona* and the only other known African genus of the family with $x = 7$, *Cleistopholis*. A comparison between the karyotypes of these two genera exposed to sequential DAPI and CMA staining reveals very different banding patterns and the presence of different heterochromatin types (Fig. 1). This confirms morphological and palynological information (Le Thomas, 1980, 1981; Hesse et al., 1985), which suggests an isolated position of this genus in a generic group together with *Lettowianthus, Piptostigma* and *Anaxagorea* (see p. 110).

Considering the position of the *Annona* tribe as a whole, one is led to the ***Annona* subfamily**, circumscribed by Walker (1971a) only on the basis of palynological (LM) criteria. This subfamily is still difficult to characterize in morphological or karyological terms, but its naturalness is being confirmed by a broadening spectrum of ultrastructural pollen details (Le Thomas, 1980, 1981; many unpublished findings from our Vienna group) and phytochemical data (Leboeuf et al., 1982). Adding all available karyological, morphological and chorological information, we can propose a working hypothesis about the differentiation of this *Annona* subfamily (Fig. 3), in which the nearly exclusively African *Hexalobus* tribe apparently occupies a central position. This informal tribe does not correspond to any of the formerly described suprageneric taxa of Annonaceae and exhibits an enormous diversity, particularly in flower characters. Still, its loose coherence is signalled by several features: hairs simple, flowers axillary, carpels ± numerous, free (or one carpel: Leins & Erbar, 1980, 1982), each with several to many ovules/seeds, chromosome base number $x = 8$.

The *Hexalobus* tribe includes the African genera *Hexalobus, Asteranthe, Ophrypetalum, Dennetia, Uvariastrum, Mischogyne, Uvariodendron* and *Uvariopsis*, which still exhibit several primitive character states; the more advanced American *Diclinanona*; and the isolated and advanced African genera *Monodora* and *Isolona*, each of which obviously should be placed in a separate tribe.The affinities between *Hexalobus* and *Diclinanona* are here illustrated by their very similar pollen tetrads (Fig. 4) and suggest a transatlantic link from Africa to South America. Another such link can be assumed between African progenitors of the *Hexalobus* alliance and the coherent southeastern North American tribe that includes *Asimina* and *Deeringothamnus* (Walker, 1971a; Raven & Axelrod, 1974). This group is relatively primitive and has a unique epidermis ultrastructure (Morawetz & Waha, 1984), $x = 8$, and much larger pollen tetrads.

Both the *Annona* and the *Cymbopetalum* tribes are predominantly or exclusively American (Fig. 3) but apparently cannot be linked to any of the other neotropical Annonaceae groups. Instead, their affinities are clearly with the more primitive members of the African *Hexalobus* tribe, but both are much more advanced in different ways. The *Annona* tribe is characterized by flowers extra-axillary, carpels fused in fruit and with one basal ovule only, chromosome base number $x = 7$ (derived from $x = 8$: see Morawetz, 1986), pollen grains in larger tetrads (or secondarily single) with more elaborate columellae and proximal exine openings. The *Cymbopetalum* tribe (sensu Walker, 1971a) corresponds closely to the *Trigynaea* group (sensu Fries, 1959) and includes the neotropical genera *Cymbopetalum, Cardiopetalum, Porcelia, Trigynaea*, and *Hornschuchia* (but not the American *Bocagea* and the Southeast Asian *Disepalum*). They share the advanced characters of extra-axillary flowers (on jointed pedicels without bracts), a chromosome base number of $x = 9$ and pollen in polyads (Fig. 5), but have retained free carpels with ± numerous ovules. Thus, it is tempting to regard the *Annona* and the *Cymbopetalum* tribes as divergent and very clearly neotropical derivatives of progenitors close to what constitutes today the African *Hexalobus* tribe.

Among the more primitive Annonaceae with single and monosulcate pollen grains, the genus ***Anaxagorea*** is a member of the so-called *Fusaea* subfamily (Walker, 1971a); it has been recently monographed by Maas & Westra and collabo-

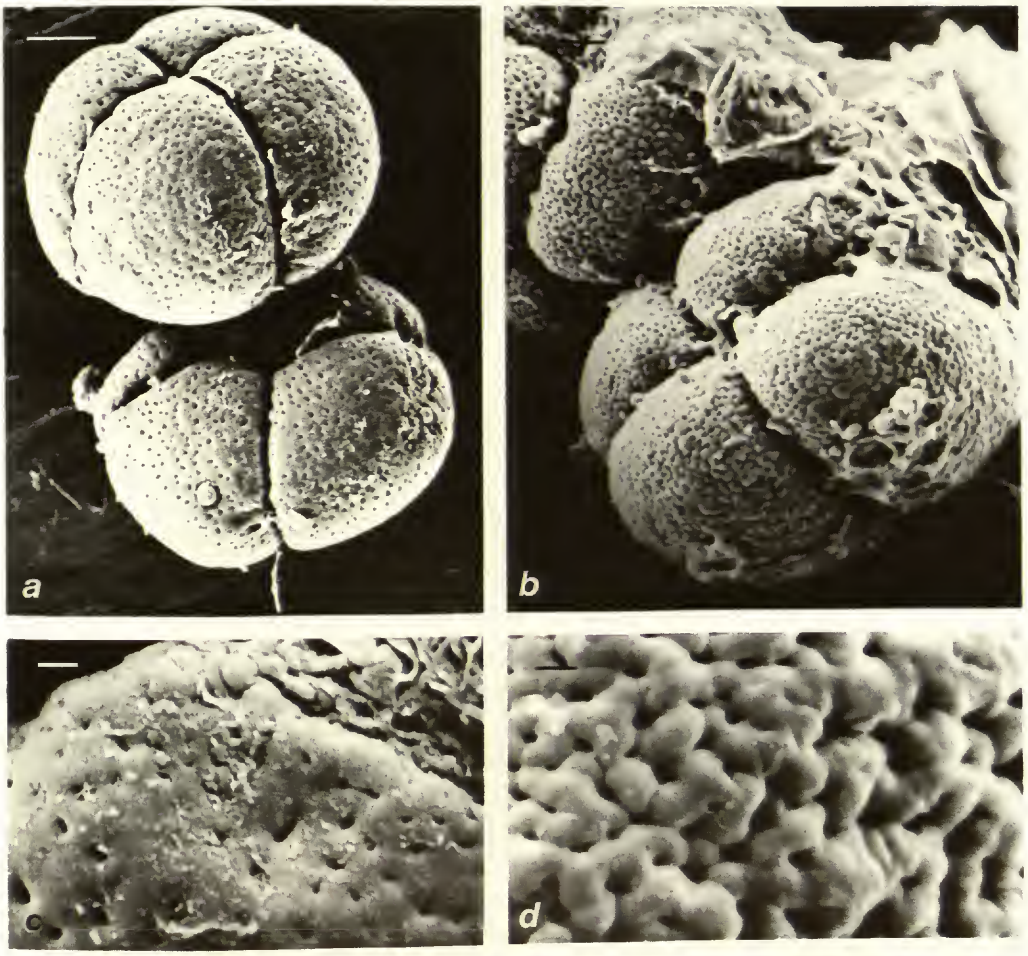

FIGURE 4. Tetragonal pollen tetrads and details of exine surface in Annonaceae (SEM). *Hexalobus* spec.—a. Tetrads (about 65 μm diam.).—b. Tetrads (about 85 μm diam.).—c. Exine (smooth, with small perforations). *Diclinanona* spec.—d. Exine (rugulate, with larger perforations). Bars 10 μm in a and b, 1 μm in c and d. (Originals from M. Waha.)

rators (1985) and is one of the most remarkable genera of the family, with about 20 species in the tropical Americas and three in Southeast Asia (Fig. 6). From former taxonomic arrangements (Fries, 1940, 1959) with two sections (or even genera), one in the Neotropics and the other in the Paleotropics, the idea of an "artificial" assembly seemed likely. But detailed studies of morphological, anatomical, palynological, karyological, and phytochemical features (Maas & Westra, 1985 with collaborators; Hesse et al., 1985) have undoubtedly demonstrated the coherence of all species of *Anaxagorea* as well as the clear separation and relative isolation of the genus within the family. Both neo- and paleotropical species have the same, very characteristic monocarps and seeds, solitary sulcate pollen grains with a ± granular exine and a peculiar extruding intine, similar nuclear structures, a chromosome base number of $x = 8$ (with $2x$ and $6x$ known), an alkaloid spectrum including the rare 7-substituted aporphines (Table 1), etc. Even more remarkable are the results of a broadly based cladistic analysis (Koek-Norman & Zandee in Maas & Westra, 1985). It is clear from several independent approaches that within the Southeast Asian group of species there is a deep hiatus: *A. javanica* and *A. luzonensis* (Fig. 6) form a closely related and somewhat isolated group (B), but still exhibit more affinities to a species group

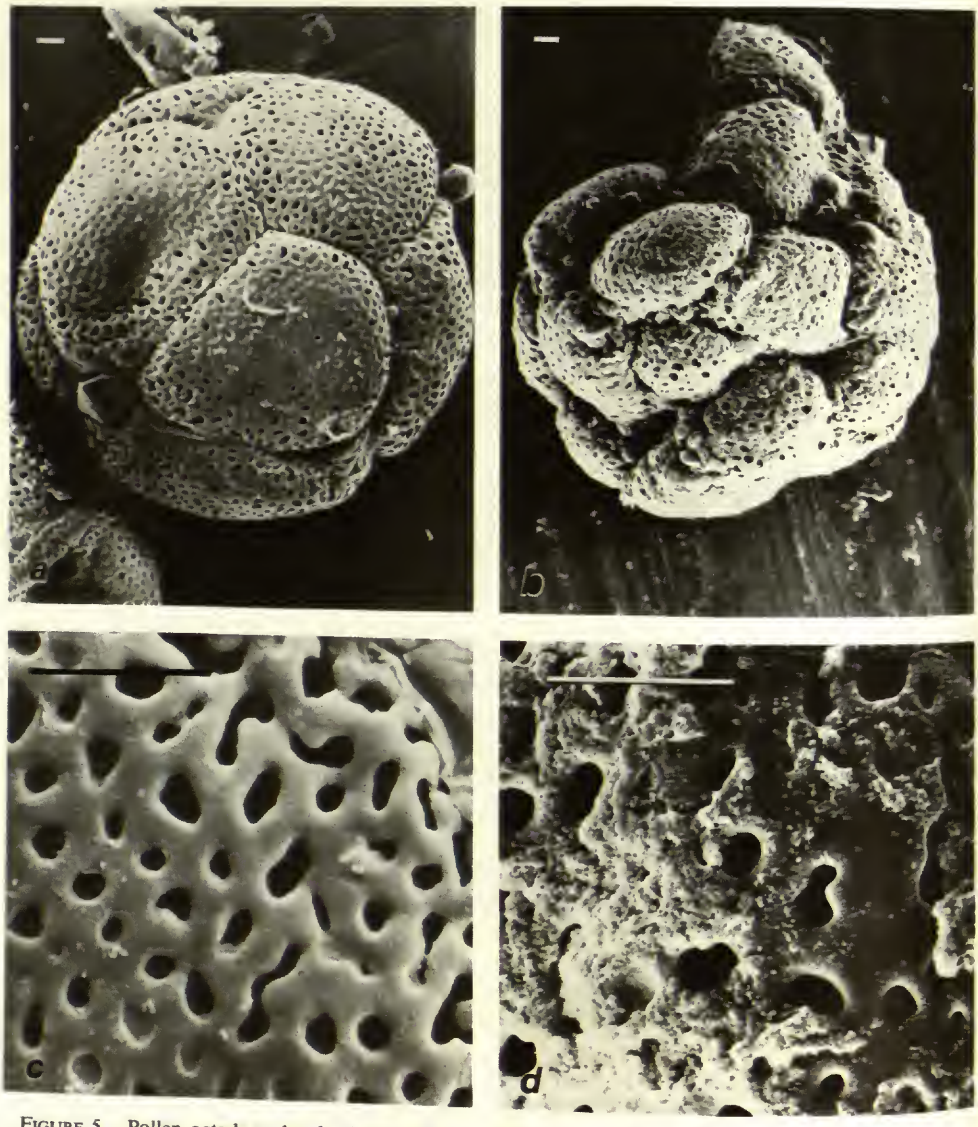

FIGURE 5. Pollen octads and polyads, and details of exine surface in Annonaceae (SEM). *Cardiopetalum calophyllum*:—a. Octads (about 100 μm diam.).—c. Exine (reticulate, with large lumina). *Porcelia goyazensis*: —b. Polyads (about 100 μm diam.).—d. Exine (reticulate, with large lumina). Bars 10 μm. (Originals from M. Waha.)

(A) centered in northern South America than to the Borneo endemic *A. borneensis*, which in turn comes much nearer to another neotropical group (C), ranging from Minas Gerais to the Amazonas Basin. A fourth group (D) is limited to the Neotropics and appears principally in central and northwestern South America. This suggests that there must have been two independent migration links (circum-North Pacific?) between the neo- and paleotropic members of *Anaxagorea*.

If one considers the affinities of *Anaxagorea* within Annonaceae on the basis of morphology, palynology (LM and EM), and—as far as known—also of karyology and phytochemistry (Hesse et al., 1985), predominantly African relationships become apparent (Fig. 7). Relatively close are

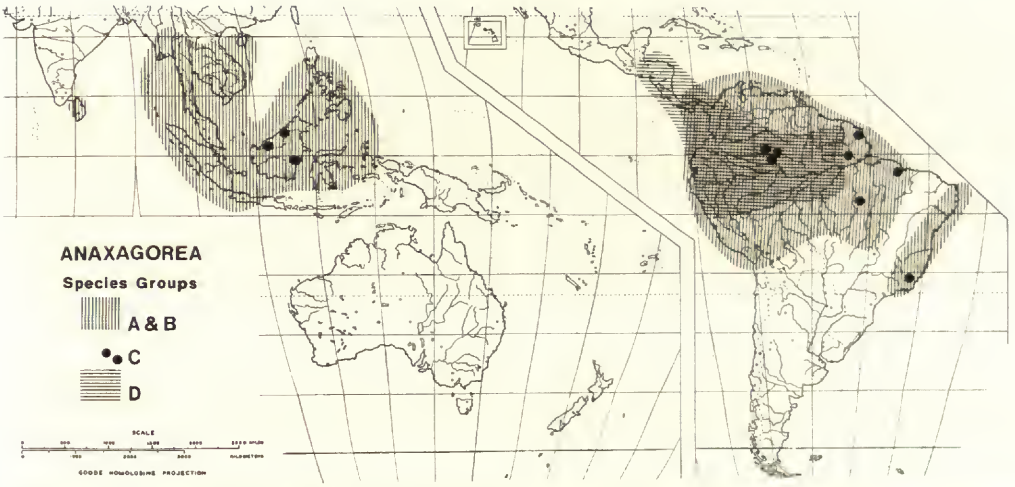

FIGURE 6. Distribution of related species groups of *Anaxagorea* in the New and Old World tropics (from data in Maas & Westra, 1985). Group A with *A. brachycarpa, A. dolichocarpa, A. gigantophylla, A. petiolata, A. manausensis, A. acuminata, A. pachypetala, A. phaeocarpa, A. brevipes,* and *A. rufa* in northern South America, and group B with *A. javanica* and *A. luzonensis* in Southeast Asia, are related. Groups A and B link to group C on the one hand with *A. angustifolia, A. prinoides,* and *A. silvatica* from the Amazonas Basin to Minas Gerais and with *A. borneensis* in Borneo, and to group D on the other hand with *A. allenii, A. crassipetala, A. guatemalensis, A. panamensis, A. macrantha, A. floribunda,* and *A. brevipedicellata* in Central and northwestern South America.

the monotypic West African *Meiocarpidium, Polyceratocarpus* with several species in West and East Africa, and the monotypic East African *Letowianthus*; somewhat more remote are the small African genera *Piptostigma* and *Cleistopholis.* They all share with *Anaxagorea* quite "primitive" morphological and palynological characters (Hesse et al., 1985)—e.g., solitary pollen grains with distal sulcus and ± undifferentiated, noncolumellate, microperforated exine—and could be grouped into a "natural" *Anaxagorea* tribe (= "*Fusaea* subfamily/tribe I"). Le Thomas (1984) has clearly demonstrated one main center for this group in tropical West Africa; a secondary center would be represented by *Anaxagorea* itself in northern South America. Thus, the proposed *Anaxagorea* tribe suggests a very ancient transatlantic (western Gondwanaland) link within the family (Figs. 6, 7).

Even more prominent relationships connect some groups of Annonaceae in Africa (and the

TABLE 1. Occurrence of 7-substituted aporphines with an alcoholic hydroxyl or an O-methyl ether group in cis (α) or trans (β) configuration, and of 6-N-oxides among several genera of Annonaceae. From data presented in Leboeuf et al., 1982.

	7-			6-N-
	OHα	OHβ	OMeβ	oxy
Anaxagorea, x = 8	+			
Cananga, x = 8	+			
Polyalthia, x = 9	+	+		
Greenwayodendron		+	+	+
Enantia, x = 8		+	+	+
Isolona, x = 8		+	+	+

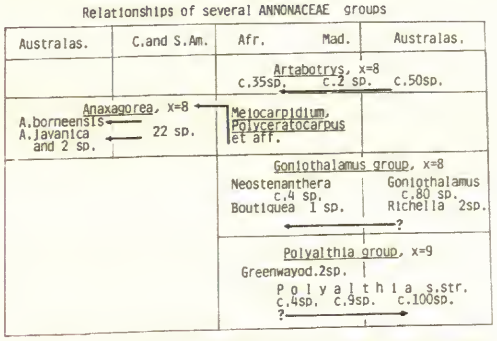

FIGURE 7. Representation of several Annonaceae groups in Central and South America, Africa, the Malagasy area, and Australasia, with suggestions about major phytogeographical links and their direction (arrows). (x = chromosome base numbers, sp. = approximate species numbers.)

Malagasy region) and in Australasia (Fig. 7). The very large genus *Polyalthia* forms the core of a group which apparently is linked to the *Anaxagorea* tribe, but exhibits the advanced chromosome base number $x = 9$. There is a remarkable range of palynological diversity (apertures from sulcate to ± inaperturate, exine elaboration from granular to fully columellate, etc.; Le Thomas, 1980, 1981; Hesse and collaborators, unpubl.), which suggests a trend from Africa to Australasia. On the other hand, the reverse trend from Australasia towards Africa is more likely for the *Goniothalamus* group of genera (also placed into the "*Fusaea* subfamily" by Walker, 1971a) with pollen tetrads, lack of distal apertures, $x = 8$, and distinctive morphological features (Hesse et al., 1985). The same also can be said about the very characteristic genus *Artabotrys*, probably a member of the *Uvaria* tribe (sensu Walker, 1971a).

Winteraceae

The Winteraceae are a small (only 4–8 genera: Vink, 1985) and isolated relic family of the Magnoliidae, formerly Magnoliales, now often placed into a separate order (Winterales: Walker & Walker, 1984). Their present distribution is centered in the tropical western Pacific (with 4 genera, only recently united into one: Vink, 1985, in New Caledonia), from where it extends to Indomalesia, eastern Australia and Tasmania, New Zealand, South and Central America, and Madagascar. Findings of the characteristic tetrad pollen date the Winteraceae back to the Lower Cretaceous and document a formerly much wider distribution (e.g., in the Antarctic, in South Africa and the northern margin of the African shield in Israel, etc.: Martin, 1978; Walker et al., 1983; Coetzee & Muller, 1984: with distribution map). With the exception of the dioecious *Tasmannia* with $x = 13$ (paleo-4x?) all other genera studied so far are high paleopolyploids based on $x = 43$, with $2n = 86$ or even $2n = 172$ (Ehrendorfer, 1980). No karyological data are available so far from ***Takhtajania perrieri***, the only and stenoendemic Winteraceae in northeastern Madagascar (known with certainty from the type locality only, and possibly extinct). This species, originally described as a member of the tropical western Pacific genus *Bubbia* (Capuron, 1963), has several distinct features and is evidently better regarded as a separate genus. On the assumption that it has a coenocarpous gynoecium consisting of two completely fused carpels, *Takhtajania* was later made the sole representative of a subfamily or even family (Leroy, 1978, 1980; Vink, 1978). In view of the plasticity of single carpel differentiation demonstrated by comparative morphological studies on other Winteraceae (Leinfellner, 1965, 1966a, 1966b; Tucker & Sampson, 1979) and related Magnoliidae (e.g., Annonaceae, *Monodora*: Leins & Erbar, 1980, 1982), I still prefer the original "one carpel" interpretation for the gynoecium of *Takhtajania*. Therefore, I regard the genus as more closely related to *Bubbia* and other Winteraceae with $x = 43$ and as a relic of a formerly more extensive African distribution of the family.

Laurales

The Laurales represent a complex of families whose interrelationships are still poorly understood. In addition to morphological, anatomical and palynological data (e.g., Cronquist, 1981), information on the ultrastructure of sieve-elements (Behnke & Barthlott, 1983) and on the karyological features (Ehrendorfer et al., 1968; Goldblatt, 1974, 1976, 1979; Okada, 1975; Okada & Tanaka, 1975; Morawetz, 1986; etc.) has broadened the approach to this problem. A survey of all families of Laurales (except Austrobaileyaceae, apparently a link with Magnoliales), together with notes on their taxonomic differentiation and distribution, is presented in Table 2. All genera are listed for which data on chromosome number, and partly also on karyotype, chromosome condensing behavior, interphase nuclear structure, etc., are available.

Formerly, **Trimeniaceae** (with a few species of *Trimenia* and *Piptocalyx* in Australasia) have been regarded as members of the Monimiaceae or at least as closely related. The finding of a diploid number ($2n = 16$) of very large submetacentric chromosomes and characteristic interphase nuclei (dark-staining euchromatin, very small chromocenters: = "*Hedyosmum* type"; **a**, Table 2) has not only substantiated the separate status of Trimeniaceae relatively far from Monimiaceae but also has given strong support to earlier suggestions about close relationships to **Chloranthaceae**, in particular to *Hedyosmum*, with the same aberrant karyological features (Morawetz, 1986). In Table 2 the two families form group I, both with $2x$ numbers on $x = 8$ (and with additional paleopolyploids in Chloranthaceae) and with S-type sieve plastids. In respect to intercontinental relationships within

TABLE 2. Suggestion for a more "natural" arrangement of taxa within the order Laurales with particular consideration of karyological data (from Morawetz, 1986). Taxa: family groups (I–IV), families, generic groups (A, B, . . . a, b, . . .) and genera. Main distribution areas: AA = southern (antarctic) South America (Chile, southern Argentina); AF = Africa; AS = Australasia; ES = East and Southeast Asia; MG = Malagasy region; NA = North America; PT = Pantropics; SA = South and Central America; SR = Sri Lanka (Ceylon). Types of interphase nuclei (in: **a–e**), and haploid chromosome numbers (*n*). For further explanations see text.

Taxa	in	*n*
I) Trimeniaceae (AS)		
Trimenia	**a**	8
Piptocalyx	**a**	8
Chloranthaceae		
a) *Hedyosmum* (SA, ES)	**a**	8
b) *Sarcandra* (ES)		15
Chloranthus (ES)		14, 15, 30
c) *Ascarina* (incl. *Ascarinopsis*; AS, MG)		14
II) Amborellaceae		
Amborella (AS)		13
III) Calycanthaceae		
Chimonanthus (ES)	**e**	11
Calycanthus (NA)	**e**	11
Idiospermaceae		
Idiospermum (AS)		11
IV) Lauraceae (PT)		
A) Many genera	**e**	12, 24, 36
B) *Cassytha*	**e**	24
Hernandiaceae sensu lato		
A) *Hernandia* sensu lato (PT)	**c**	10, 20, 40
B) *Sparattanthelium* (SA)	**c**	ca. 24, ca. 48
C) *Gyrocarpus* (PT)	**e**	15
V) Gomortegaceae		
Gomortega (AA)		21
Atherospermataceae		
a) *Atherosperma* (AS)		ca. 21
b) *Doryphora* (AS)	**b**	ca. 41
Laurelia (AS, AA)		22
Daphnandra (AS, AA)		22
Siparunaceae		
Siparuna (SA)		22, 44
Monimiaceae s. str.		
A) *Hortonia* (SR)	**d**	19
B-a) *Peumus* (AA)	**d**	38
-b) *Monimia* (MG)		ca. 44–48
C-a) *Xymalos* (AF)	**d**	19
-b) *Palmeria* (AS)		19
-c) *Hedycaria* (AS)	**d**	19
Levieria (AS)	**d**	19
-d) *Ephippiandra* (MG) (including *Hedycaryopsis*)	**d**	21
Tambourissa (MG)		19
-e) *Kibara* (AS)		22
Tetrasynandra (AS)		ca. 43
-f) *Wilkiea* (AS)		ca. 38
Mollinedia (SA)	**d**	ca. 18, 19, 20; ca. 50, 90
-g) *Hennecartia* (SA)	**d**	ca. 48

the extremely old and primitive Chloranthaceae, it is interesting to note the close affinities between the bulk of *Ascarina* species (11) in Australasia and the single representative in Madagascar (formerly *Ascarinopsis*, now *Ascarina coursii*: Jérémie, 1980). The relic nature of these extant populations is shown by the fact that several different fossil *Ascarina* pollen types have been found from the Paleocene (and possibly even earlier, from the Cretaceous) to the Miocene, ranging from Australia and New Zealand via submersed ridges in the Indian Ocean to South Africa (Coetzee & Muller, 1984: with distribution map).

The family groups II, III and IV (Table 2) exhibit secondary chromosome base numbers of $x_2 = 10, 11, 12, 13$, and 15, which may be the result of a differentiation at the $4x$ (or $3x$?) level. The relic and monotypic ***Amborella*** (II) from New Caledonia has $2n = 26$ and chromosomes much smaller than in Trimeniaceae and *Hedyosmum*. There are S-type sieve elements present, in contrast to the following III- and IV-families, in which only the P-type has been found. **Calycanthaceae** and **Idiospermaceae** form a clearly related family pair (III), documenting an ancient relationship between Southeast Asia and North America on the one hand, and northeastern Aus-

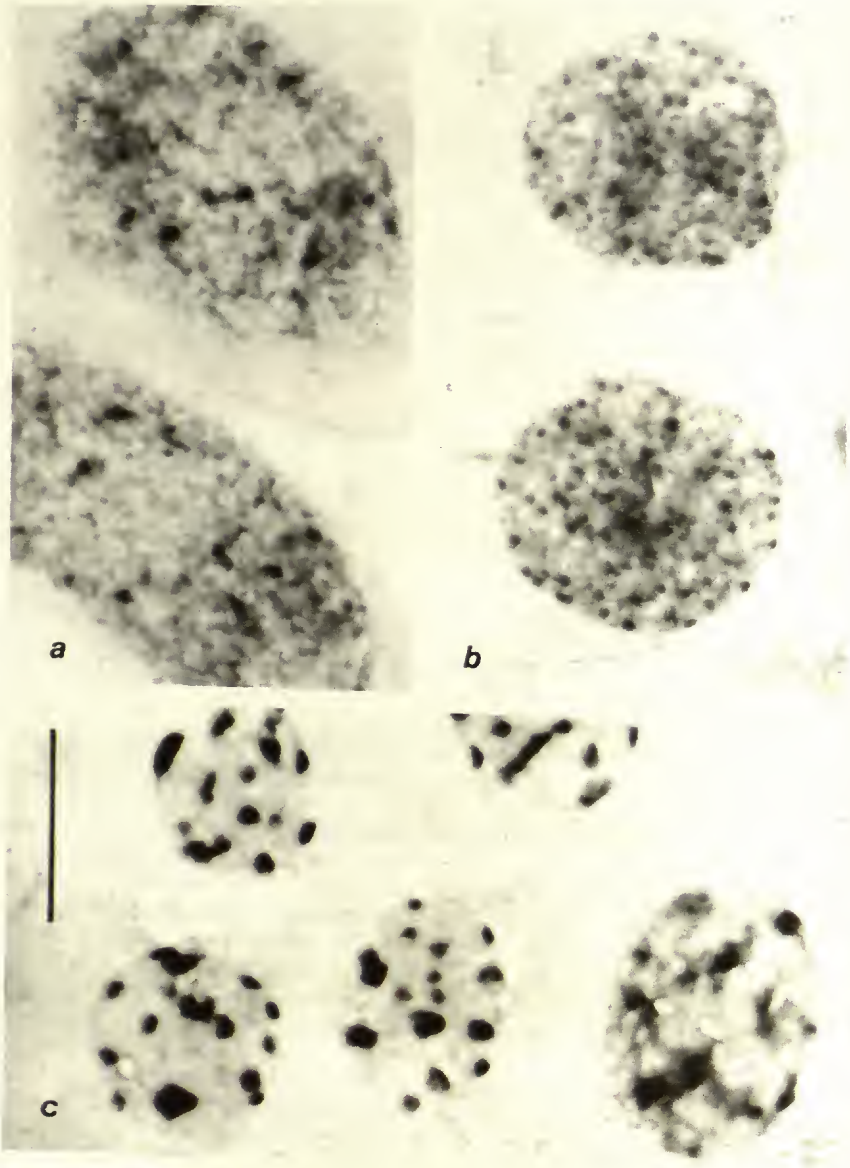

FIGURE 8. Interphase nuclei in Hernandiaceae sensu lato.—a, *Hernandia* spec. ($2n$ = 40), and b, *Sparattanthelium botocudorum* ($2n$ = ca. 96), with reticulate type (small chromocenters).—c. *Gyrocarpus americanus* subsp. *pachyphyllus* ($2n$ = 30) with prochromosomal type (large chromocenters). (From Morawetz, 1986.)

tralia on the other. Their large prochromosomal interphase nuclei (barely stained euchromatin, large chromocenters: "*Gyrocarpus* type"; Fig. 8, c; Table 2, e) link groups III and part of IV with Lauraceae and some of the Hernandiaceae sensu lato (Table 2, C). Whereas **Lauraceae** are very uniform and homogeneous in their karyology, there is much heterogeneity in the **Hernandiaceae** sensu lato. The three genera studied so far differ not only in their chromosome base number, but also in their interphase nuclei. In contrast to *Gyrocarpus* (type **e**), they are of the reticulate type (well-stained euchromatin, small chromocenters: "*Hernandia* type"; Fig. 8, a; Table 2, c) in *Hernandia* sensu lato (Table 2, A) and *Sparattanthelium* (Table 2, B) (Morawetz,

1986). This finding is a warning against the customary segregation of *Hernandia* into Hernandioideae (or Hernandiaceae sensu stricto) and of *Sparattanthelium* and *Gyrocarpus* into Gyrocarpoideae (or Gyrocarpaceae; see Kubitzki, 1969); A, B and C are obviously of equal rank.

In the present context, it is relevant to point to the disjunct pantropical distribution of taxa within *Hernandia* and *Gyrocarpus,* which Kubitzki (1969, 1975) has discussed on the basis of a careful character analysis. Among the 24 species of *Hernandia,* centers of primitive characters are found in the western Pacific and the Malagasy region. Representatives of the *H. ovigera* group link these areas and have managed to reach Central America during an older expansion phase. A switch from zoochory to hydrochory has made possible a more recent expansion phase from Australasia into coastal areas of various Pacific islands and of East Africa, and from Central America to coastal West Africa. A similar expansion from Australasia towards Africa and Central America is apparent for the subspecies of *Gyrocarpus americanus.*

Finally, the family group V (Table 2) is characterized by still higher paleopolyploid (probably $6x$) base numbers, mostly in the range of $x_3 =$ 19–22. There are numerous other features which help to delimit group V, e.g., the presence of abundant endosperm in the ripe seeds (lacking in groups III and IV). The relic and monotypic **Gomortegaceae** always have been recognized as a separate family; their place is obviously closer to Atherospermataceae than to Lauraceae (Goldblatt, 1976). Up to the present the remaining families often have been treated only as subfamilies of Monimiaceae sensu lato, but sieve-tube plastids are of the P-type in Gomortegaceae, Atherospermataceae, and Siparunaceae, and of the S-type in Monimiaceae sensu stricto. Other characters correlate with this, e.g., valvate anthers, chromosome number $x_3 = 21$–22 and larger, versus predominantly $x_3 = 19$ and smaller. Interphase nuclei exhibit ± well-stained euchromatin, but have few and large chromocenters in Atherospermataceae ("*Doryphora* type"; **b**, Table 2) versus numerous and minute ones in Monimiaceae sensu stricto ("*Mollinedia* type"; **d**, Table 2) (Morawetz, 1986).

The rather primitive **Atherospermataceae** (flowers partly bisexual, etc.) are today limited to the western Pacific area, from New Guinea and northwestern Australia to New Caledonia, Tasmania and New Zealand, and to southern South America. Their fossil record (wood, leaves, pollen: see Schodde, 1969; Knappe & Rüffle, 1975; Muller, 1981), however, dates back into the Upper Cretaceous of South Africa and through the Lower Tertiary extends to the Antarctic, Argentina, New Zealand, Egypt (and central Europe?). All this clearly illustrates the long history of a formerly much more widespread southern hemisphere family.

The fossil record is much less satisfactory for the more advanced **Monimiaceae** sensu stricto (flowers nearly always unisexual, etc.), but the depauperate nature of the family (isolated genera, few species, disjunct distribution patterns) suggests a similar history as for Atherospermataceae. The isolated genera *Hortonia* (a few species in Sri Lanka) and the monotypic *Peumus* (in Chile) are usually regarded as representatives of separate subfamilies, Hortonioideae (A) and Monimioideae (B-a). For *Peumus,* with $2n = 78$ ($x_5 = 39$, possibly $12x$), Morawetz (1981) has demonstrated a strongly repatterned and completely diploidized karyotype. *Monimia* (B-b), with three species in the Mascarene Islands, has been linked with *Peumus* because of certain similarities in basal stamen appendages, spinulose pollen grains, etc. (Thorne, 1974; Lorence, 1985). Still, flower structures and chromosome numbers are so different in *Monimia* as to make any closer kinship unlikely. Certainly, there are no direct relationships with the other endemic Malagasy genera of the family (C-d) or with the African *Xymalos* (C-a).

The remaining Monimiaceae sensu stricto are now grouped under subfamily Mollinedioideae (C; Thorne, 1974), but the genus *Xymalos* (C-a) from tropical Africa and the Cameroon Mountains is so aberrant (only one carpel per female flower, broad, caplike stigma, etc.) that it certainly would also merit placement in a separate subfamily. Nevertheless, other characters clearly demonstrate its affinity with Monimiaceae sensu stricto, e.g., chromosome number $2n = 38$ and nucleotype (Morawetz, 1986).

The following generic groups (C-c and C-d, Table 2) have female flowers with broad receptacles and numerous short-styled carpels, ± covered and connected by mucilage, serving as a pollen-transmitting medium (Endress, 1980). The loosely coherent group C-d from the Malagasy region comprises *Decarydendron* and *Ephippiandra* (including *Hedycaryopsis*), endemic on Madagascar, and *Tambourissa* (including *Phanerogonocarpus* and *Schrameckia*), also on the

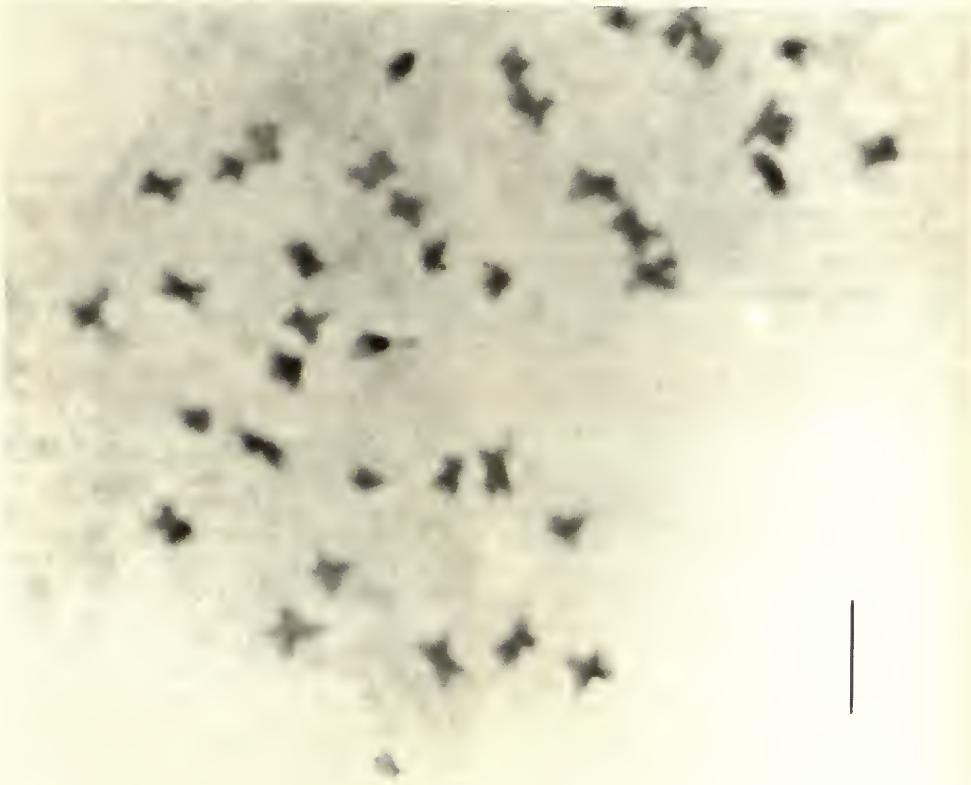

FIGURE 9. Mitotic metaphase chromosomes of *Tambourissa* spec. (Monimiaceae; Madagascar), $2n = 38$. Giemsa staining; scale 5 μm. (Original from Morawetz, 1986.)

Mascarene Islands and the Comores. These genera are fairly well covered by morphological (Endress & Lorence, 1983) and palynological studies (Lorence et al., 1984), and by a recent monograph (Lorence, 1985). This group C-d is characterized by simple hairs, monoecious flowers, the male with numerous ± sessile stamens on open to ± closed and then radially splitting receptacles, the female flowers with flat to utriculate and then "hyperstigma"-forming receptacles (which never open by circumcision!), and with short-styled free to submerged carpels. For *Ephippiandra* (= *Hedycaryopsis*) *madagascariensis* $2n = 42$ has been found, whereas *Tambourissa* apparently has $2n = 38$ throughout (Fig. 9; Morawetz, 1986; Lorence, 1985). Relationships of this Malagasy group are evidently only with the less advanced Australasian genera *Hedycarya, Levieria* (both $2n = 38$), and *Kibaropsis*, which form group C-c. They differ in their monoecious to mostly dioecious flowers with flat to ± cupuliform receptacle, opening without splitting or circumcision, and the female flowers never with "hyperstigma" or submerged carpels. The Australasian *Palmeria* (C-b), also $2n = 38$, may be a forerunner of groups C-c and C-d because it still develops long-styled carpels with individual stigmata and lacks pollen-transmitting mucilage.

The remaining groups of Mollinedioideae (C-e, -f, -g) are even more advanced in their flower morphology and extend from the western Pacific into the Neotropics. Their female receptacles enclose the short-styled, mucilage-covered carpels and form ± perfect "hyperstigmata" (Endress, 1980); in groups C-e and C-f they open by circumcision after flowering. The Australasian *Kibara* group (C-e) has male flowers which develop 4–8, ± connivent stamens with ± long filaments in 1–2 cycles at their center, and includes the genera *Matthaea, Kibara* ($2n = 44$), *Steganthera, Tetrasynandra* ($2n =$ ca. 86), *Anthobembix*, and

possibly *Lauterbachia*. In the *Mollinedia* group (C-f) the male flowers have more numerous and ± sessile stamens, which are dispersed over the inner surface of the receptacle. This group has monoecious representatives in Australasia—*Wilkiea* ($2n$ = ca. 76), *Austromatthaea*, and *Kairoa*—and dioecious members in the American Tropics—*Mollinedia* (including *Macropeplus*; $2n$ = ca. 36, 38, 40, ca. 100, 180: Morawetz, 1986) and *Macrotorus*. Groups C-e and C-f are certainly related, but C-f with the monotypic genus *Hennecartia* in tropical eastern South America is aberrant in its extremely utriculate and "hyperstigmatic" female flowers, the discoid male flowers with numerous ± sessile stamens and anthers opening by an equatorial slit, and chromosome number $2n$ = ca. 96 (Morawetz, 1986). *Hennecartia* apparently has independent links with Australasian Mollinedioideae (C-c?).

Finally, **Siparunaceae**, with unisexual and cupuliform flowers, are more advanced than the apparently related Atherospermataceae, as has already been mentioned. Its main center of differentiation is in the Neotropics with the large and polymorphic genus *Siparuna* ($2n$ = 44, 88). There is, however, the clearly more advanced anisophyllous genus *Glossocalyx* in tropical West Africa, another example for a transatlantic link.

Rutaceae

The Rutaceae are a large family with ca. 150 genera, about 1,500 species, and a worldwide, tropical to temperate distribution. Here again, the last complete systematic treatment (Engler, 1931) proves to be largely formal and "artificial," now demonstrated by recent studies on morphology and anatomy (Hartl, 1957; Gut, 1966; Corner, 1976; Boesewinkel, 1977), karyology (Guerra, 1980, 1984a, 1984b, 1986; Ehrendorfer, 1982), comparative phytochemistry (Waterman, 1975; Waterman & Grundon, 1983; Fernandes da Silva et al., in prep.). Gradually a broader and more "natural" approach to Rutaceae systematics is being achieved, and consequently more realistic phytogeographical conclusions are possible.

First, a few comments on the interesting relationships among members of the relatively large and primitive, pantropical to warm temperate genus ***Zanthoxylum*** (including *Fagara*). This includes about 250 species and has a fossil record from the early Tertiary onward, e.g., in North America (Tiffney, 1980) and central Europe (Gregor, 1975, 1984). Chromosome numbers can be interpreted as basically paleo-4x ($2n$ = 36, x = 9), but most species are 8x (and up to 12x, 16x), and there is also descending dysploidy (e.g., $2n$ = 72 → 70 → 68 → 66 → 64). On the basis of alkaloid derivatives of the 1-benzyltetrahydroisoquinoline, furoquinoline and acridone types, of canthin-6-ones, amides and coumarins, etc., Fish & Waterman (1973) have discussed the evolutionary relationships of the *Zanthoxylum-Fagara* complex. It is clear that neotropical representatives (mainly subsections *Paniculatae-Neogaeae* p.p. and *Pterota*) exhibit the least advanced profiles of secondary compounds (and flower characters) and occupy a central and basic position within the genus. From the accumulation of phenylethylamines, aporphines, ortho-coupled benzophenanthridines, protoberberines, etc. (and morphology), it is apparent that the closest ties are between *Paniculatae-Neogaeae* and the African members of *Paniculatae-Gerontogaeae*, which in turn can be linked to Asian taxa of this group. The Australasian sect. *Blackburnia* apparently represents a direct offshoot from *Paniculatae-Neogaeae*, with the Argentinian *Zanthoxylum coco* suggesting a possible connection. These links suggest corresponding migration routes.

The variable monotypic ***Toddalia*** *asiatica* is clearly related to *Zanthoxylum* sensu lato (and not to other Toddalioideae sensu Engler, 1931) as indicated by phytochemistry (formation of aporphines), karyology ($2n$ = 36, 72; structure of metaphase nuclei), and morphology (prickles). The present distribution of *Toddalia* ranges from tropical Southeast Asia to Japan, India, East and South Africa, but it has a fossil record in West Africa and Europe as well (Gregor, 1979). It may have had an African center of origin.

Fagaropsis (syn. *Clausenopsis*) today is widespread, with ca. four ± deciduous species in relatively dry upland forests of tropical Africa and Madagascar. Fossil seeds of *Fagaropsis* are known from the European Eocene and Miocene (Gregor, 1984). The genus has been variously placed near *Clausena* (Aurantioideae), *Vepris*, or *Phellodendron* (both "Toddalioideae"). The latter position, proposed by Engler (1931) with hesitation, is now strongly backed by a remarkably similar phytochemical profile (Waterman & Khalid, 1981: table 2). ***Phellodendron***, limited with about 10 extant deciduous species to subtropical and temperate East Asia, has a fossil record from the older Tertiary (Oligocene) onward, including Eu-

FIGURE 10. Mitotic metaphase chromosomes of *Phellodendron amurense* (Rutaceae), $2n = 78$. Feulgen and aceto-carmine staining; scale 5 μm. (From Guerra, 1980.)

rope and eastern North America (Tiffney, 1980). This suggests a formerly ± continuous northern hemisphere distribution. *Phellodendron* has a characteristic karyology and an odd paleo-(hyper)8*x* chromosome number of $n = 39$ (Fig. 10; Guerra, 1980, 1984a). Parallel chromosomal data for *Fagaropsis* are still lacking but should help to demonstrate the closer relationship of the two genera and a possible African, tropical-montane origin of *Phellodendron* from *Fagaropsis*-like progenitors.

The genera of Rutaceae listed in Table 3, with remarks on chorological, karyological and phytochemical features, have been widely separated in Engler's system (1931), i.e., in Xanthoxyleae-Evodiinae (*Evodia* to *Geijera*) with capsular fruits, and in Toddalieae-Toddaliinae (*Halfordia* to *Araliopsis*), -Oriciinae (*Oricia* and *Diphasia*), and -Amyridinae (*Teclea*) with drupaceous fruits. A provisional arrangement in two closely related informal tribes is supported by various similarities: woody and mostly evergreen plants without

TABLE 3. Suggestions for a more "natural" arrangement of some Rutaceae genera into an *Evodia*- and an *Acronychia* tribe, with particular reference to karyological data (from Guerra, 1980, 1984, 1986)—haploid chromosome numbers (*n*) and types of interphase nuclei (in)—and to phytochemical constituents (from Gray & Mester in Waterman & Grundon, 1983; coumarins (C), furoquinoline (F) and acridone (A) substitution patterns. Abbreviations for distribution areas as in Table 2.

				F			A		
	n	in	C	7	6 + 7	6 + 7 + 8	1–4	1–4 + 10	5–6
Evodia-tribe									
Evodia (AS, ES, MG)	**18**, 36, 38, 39	S2	+	+	+	−	+	+	−
Melicope (AS)	18	S1	+	+	+	+	+	+	−
Pelea (AS)	36	S5	+	−	+	−	−	−	−
Orixa (ES)	20	S3	+	+	+	−	−	−	−
Geijera (AS)	54		+	−	−	−	−	−	−
Halfordia (AS)			+	−	+	+	−	−	−
Skimmia (ES)	15	S4	+	−	−	−	−	−	−
Acronychia-tribe									
Acronychia (AS, ES)	17, **18**	S1	−	+	+	−	+	+	−
Vepris (AF, MG)	36	A1	−	−	+	+	−	+	−
Araliopsis (AF)			−	−	+	+	−	−	−
Oricia (AF)			−	−	+	+	−	+	+
Diphasia (AF)	36		−	−	−	+	−	+	+
Teclea (AF, MG)	36		−	−	+	+	−	+	+

prickles; leaves usually trifoliate or simple; flowers inconspicuous, 5–4-merous; gynoecium coenocarpous with 1–5 fertile loculi, each with 1–2 ovules; fruits capsular to drupaceous; seeds usually with endosperm. Both groups have lost their 2*x* members and have differentiated from $n = 18$, a secondary paleo-4*x* level. In comparison with more advanced tribes, their secondary metabolite spectrum is relatively simple. The ***Evodia*-tribe**, mostly with opposite leaves and coumarins, is less advanced in its partly 5-merous flowers and capsular fruits, the possible persistence of 1-benzyltetrahydroiso quinoline alkaloids, the simple substitution pattern in furoquinolines, and the paucity of (simple) acridones (Table 3). Its center is tropical Australasia, but *Evodia* extends into the Malagasy region, and *Pelea* is Hawaiian. Advanced members such as *Geijera* (Australia, New Caledonia), the deciduous *Orixa* (Japan), or *Skimmia* (mountains of East Asia) have become highly polyploid or dysploid. In contrast, the ***Acronychia* tribe**, mostly with alternate leaves and without coumarins, is more advanced in its usually 4-merous flowers, drupaceous fruits, and the much greater diversification of furoquinolines and acridones (Table 3). The morphology, karyology, and chemistry of *Acronychia* in tropical Australasia and Southeast Asia represents a link with the *Evodia* group. All the other genera occur in tropical Africa (but not in the Malagasy region; one species of *Vepris* also in India). These genera are even more advanced in the reduction of fertile loculi in the ovary from 4 to 2 and 1, loss of seed endosperm, switch to the paleo-8*x* level ($n = 36$) and complicated furoquinoline and acridone substitution patterns (Table 3). All this suggests a spatial differentiation and general expansion of the *Evodia* and *Acronychia* groups from Australasia towards tropical Africa.

The ***Diosma* group** (Diosmeae: Engler, 1931) is strongly differentiated in the Cape region with sclerophyllous and ericoid shrubs in about 10 genera and several hundred species. Its profile of secondary compounds is advanced (no alkaloids, some simple coumarins), its chromosome numbers (with descending dysploidy on 4*x*: $n = 18?$, 17, 15, 14, 13 and 6*x*: $n = 25$, 24, 23?, 21, 19; Guerra, 1980, 1984a) reflect very active differentiation in mediterranean habitats. The isolated genus *Calodendron* with two broad-leaved species in (sub)tropical uplands of East and South Africa

and a paleo-6x chromosome number based on $x = 9$ ($n = 27$) links the Cape genera in morphology, phytochemistry (similar limonoids), ecology, and geography with the *Evodia* group, ranging from Australasia to the Malagasy region. It is remarkable that there are similar links with the *Evodia* group and the *Boronia* group (*Boronieae*), which has differentiated in a very similar way in mediterranean Australia as the *Diosma* group in the Cape.

Finally, subfamily **Aurantioideae**, with a generally accepted circumscription among Rutaceae, includes about 30 genera and is very obviously centered in Southeast Asia, with extensions into Australasia and tropical Africa (but not into the Malagasy region). There is little karyological or phytochemical information on the few African members, but even the morphological and systematic data available clearly demonstrate several more recent to evidently quite ancient links with representatives from Southeast Asia: (a) closely related species within *Clausena* in India, Sri Lanka and East, West and South Africa; (b) obvious affinities among the more numerous and more primitive genera of the *Aegle* group in Southeast Asia (particularly *Aegle* and *Swinglea*) on the one hand, and the more advanced *Afraegle, Balsamocitrus,* and *Aeglopsis* in East and West Africa on the other; (c) more isolated position of the genus *Citropsis* in tropical Africa, with possible relationships to *Hesperethusa* and *Pleiospermium* in the otherwise ± exclusively Southeast Asian and Australasian *Citrus* group.

Dilleniaceae

Interesting worldwide relationships are being revealed within the ancient and disjunct pantropical family Dilleniaceae (for basic data see Gilg & Werdermann, 1925). A survey of karyosystematic data and a general distribution map have been presented by Ehrendorfer (1980, 1982). On the basis of morphological, anatomical and chromosomal differences, the family is divided into two subfamilies, the more heterogeneous paleotropic Dillenioideae and the predominantly neotropic Tetraceroideae. This division recently has been supported by ultrastructural palynological data (Dickison et al., 1982).

The genus ***Dillenia*** comprises ca. 60 species, mostly evergreen trees and shrubs from humid environments. It is paleopolyploid ($n = 24, 26, 27, 56$) and has its greatest diversity in the Indonesian area. Morphological (leaves, flowers) and phytochemical (flavonoids) trends suggest an old connection via Sri Lanka and the Mascarenes to Madagascar (about two species) and more recent extensions to the western Pacific islands (Fiji, etc.) and to northern Southeast Asia (Kubitzki, 1975). ***Hibbertia***, another member of the Dillenioideae, is the largest genus in the family. The approximately 150 species are mostly found in (semi)xeric habitats of Australia (and adjacent southern Malesia) and the western Pacific (New Caledonia, etc.) and exhibit a bewildering array of differentiation in respect to growth and life forms, leaf morphology and anatomy (Rury & Dickison, 1977; Dickison et al., 1978), chromosome numbers (descending dysploidy to $n =$ 5 and 4, polyploidy up to $n = 8, 9, 10, 12, 13, 16, 18, 27, 28, 32$), etc. Within the rather primitive and quite distinct sect. *Hemistemma* there is a disjunction between a group of about eight species from tropical northwestern, northern and northeastern Australia (*Alternifoliae*) and a single (but polymorphic) species in Madagascar (*Oppositifoliae*: *H. coriacea*).

The third genus represented in the African flora is ***Tetracera*** (Tetraceroideae), comprising 44 species, 15 in Africa. It has a pantropical distribution and comprises mostly ± climbing shrubs or small trees of woodland and savanna (Kubitzki, 1970). There are several records of $n =$ 14 and 13. The other genera of Tetraceroideae (Kubitzki, 1971) are neotropical and morphologically more advanced (*Doliocarpus* and *Curatella*, $n = 13$, *Pinzona* and *Davilla*, $n = 10$). The greatest diversity and concentration of primitive morphological and phytochemical (flavonoid) features within *Tetracera* occur from West Africa to Madagascar (particularly in sect. *Akara*). If this is accepted as the area of the initial differentiation of the genus, sect. *Akara* should be placed near the base of the genus and would represent a case of an early differentiation from Africa and Madagascar (seven species) towards Southeast Asia (three species). Sect. *Akara* may be linked to sect. *Tetracera* through the *T. potatoria* group, limited to Africa (four species) and Madagascar (two species), and the *T. volubilis* group. The two African species exhibit obvious morphological and phytochemical affinities to eight species in the Neotropics (predominantly in eastern Brazil) and four in Australasia. Most advanced in sect. *Tetracera* are the species allied to *T. willdenowiana* with eight species in Australasia and seven in central and northern South America. This assembly is linked to Southeast Asian members of the *T. volubilis* group through

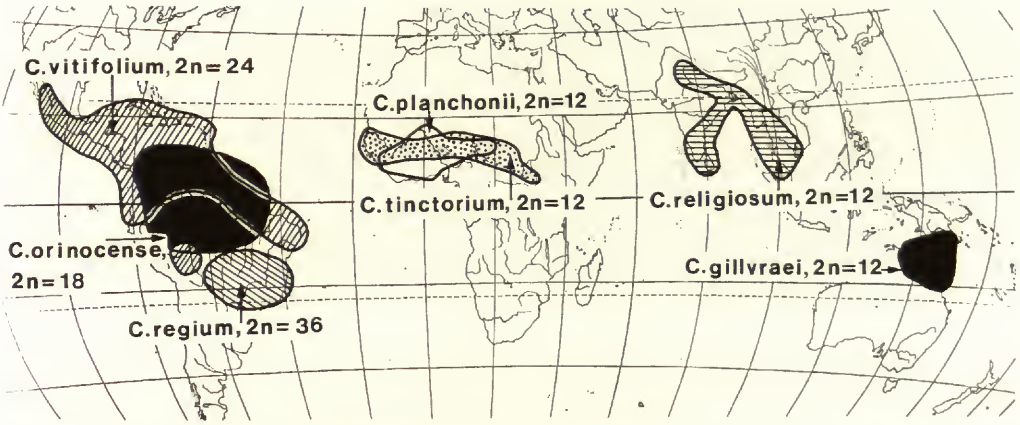

FIGURE 11. Distribution of *Cochlospermum* species for which chromosome numbers are known (7 of 12 spp.). (From Poppendieck, 1980, and Morawetz, 1986.)

T. kothalsii and *T. macrophylla.* This suggests an amphipacific connection of the neotropical members, in contrast to the *T. volubilis* group with its southern transatlantic links. It is remarkable that all the neotropical derivatives of the genus have a peculiar type of androdioecy with pollen dimorphism (by hybrid introgression?) (Kubitzki, 1970; Dickison et al., 1982).

COCHLOSPERMACEAE

According to a recent monograph (Poppendieck, 1980), the Cochlospermaceae contain two genera, *Cochlospermum* ($x = 6$), with subg. *Cochlospermum* (pantropical, 10 species) and subg. *Diploporanda* (South America, two species), and *Amoreuxia* (mainly Central America and Mexico, three species). The genus *Bixa* ($x = 7$, with a few neotropical species) is closely related, but better maintained as a separate family. Placement of Cochlospermaceae and Bixaceae into either Malvales or Violales is controversial, but a recent comparison of chromosome and nuclear structures clearly favors the latter alternative (Morawetz, 1986).

Within Cochlospermaceae there are obvious phylogenetic links from the treelike subg. *Diploporanda* (with *C. orinocense,* $2n = 18$) both to the herbaceous and otherwise advanced *Amoreuxia,* and to subg. *Cochlospermum.* This subgenus is primarily made up of tree species of dry forests in South and Central America (*C. vitifolium,* $2n = 24$), Africa (*C. angolense*), Southeast Asia (*C. religiosum,* $2n = 12$), and northern Australia (*C. gillivraei,* $2n = 12$ and *C. fraseri*) (Fig. 11). Parallel evolution has, however, resulted in the origin of suffruticose geoxylic and better fire-adapted savanna species, both in the Americas (*C. regium,* $2n = 36$) and in Africa (*C. planchonii,* $2n = 12$; *C. tinctorium,* $2n = 12$; and two other species).

In view of the concentration of the most diverse and morphologically most "primitive" taxa of Cochlospermaceae and Bixaceae in the Americas, a neotropical origin for the group can be postulated. The presence of very different $3x$, $4x$, and $6x$ taxa in this area should be regarded as the result of a long-continued differentiation, whereas only closely related $2x$ taxa have so far been found in the Paleotropics. As no clear morphological (or other) trends can be recognized among these paleotropical representatives of subg. *Cochlospermum,* we are still ignorant about the direction and age of their migrations.

RUBIACEAE

Recent multidisciplinary systematic studies including karyology (Fig. 12) and phytochemistry (Fig. 13) have furnished a new basis for the interpretation of transcontinental relationships among groups of the enormous, worldwide family Rubiaceae.

The **Naucleeae** sensu lato (Schumann, 1891) are pantropical, but clearly centered in Southeast Asia. The tribe is paleo-$4x$, based on $x = 11$, and nearly all species so far studied have $2n = 44$ (Fig. 6); *Nauclea orientalis* has $2n = 88$ (Teppner et al., 1984; Kiehn, 1985, 1986a, 1986b). There is a remarkable phytochemical diversity, particularly with respect to the intensively studied indole alkaloids, in this and other groups of Ru-

TABLE 4. Systematic grouping of the Rubiaceae—Naucleeae sensu lato (Schumann, 1891) and references to their general distribution according to Ridsdale (1975, 1976, 1978a, 1978b). Nearly all taxa are paleotetraploid on $x = 11$, $2n = 44$.

1) Naucleeae sensu stricto, 21 genera: Paleotropic
2) Mitragyneae:
Mitragyna, 10 sp.: Paleotropic
6 sp.: Southeast Asia
4 sp.: Africa
Uncaria, 34 sp.: Pantropic
29 sp.: Australasia
3 sp.: Africa
2 sp.: America
3) Cephalantheae:
Cephalanthus, 6 sp.: Pantropic (to temperate)
2 sp.: Southeast Asia
3 sp.: North, Central, and South America
1 sp.: South Africa

biaceae (e.g., Phillipson et al., 1982; Kisakürek et al., 1983). Ridsdale (1975, 1976, 1978a, 1978b) has monographed the Naucleeae sensu lato and has divided it into three, more homogeneous tribes (Table 4).

Cephalanthus, the only genus of Cephalantheae, includes six species in Southeast Asia, North Central and South America, and South Africa, which occur mostly in riverine vegetation from the (sub)tropical to the (warm) temperate zone (Ridsdale, 1976). Morphology and particularly phytochemistry (indole alkaloids: Phillipson et al., 1982) suggest that the primary differentiation of the genus occurred in Southeast Asia, where two quite distinct species, the local *C. angustifolius* in Laos and Vietnam and the widespread *C. tetrandra*, are found today. The latter exhibits rather remote links with the South African *C. natalensis* (in Natal and Transvaal) which is characterized by a specific set of indole alkaloids. On the other hand, there are very obvious affinities expressed by a set of common indole alkaloids from *C. tetrandra* in Southeast Asia towards *C. occidentalis* in eastern North America and from the latter to *C. glabratus* in eastern South America and also to *C. salicifolius* in Central America.

Mitragyna (Mitragyneae) comprises six species in tropical Southeast Asia (from New Guinea to southern China and Sri Lanka), and four species in tropical East and West Africa. Morphological progressions (e.g., the origin of corolla appendages in the African members of the *Hallea* group: Ridsdale, 1978a) and the gradual reduction in otherwise widespread indole alkaloids (C3a-, C4d- and C5b-types much more diversified in the Southeast Asian taxa, C4a-types only there; cf. Fig. 13 and Phillipson et al., 1982; Kisakürek et al., 1983) clearly suggest a migration from Southeast Asia to Africa. In the predominantly Southeast Asian *Mitragyna* species group sensu stricto, the only African member, *M. inermis*, could be regarded as a link with the exclusively African *Hallea* group (three species) which shares a very similar set of C3a, C4d and C5b indole alkaloids.

Uncaria, also a member of the Mitragyneae, is clearly centered in Australasia, where there are 29 species; only two occur in Central and (predominantly northwestern) South America, and three in tropical Africa and Madagascar (Ridsdale, 1978a). From the morphological and phytochemical data (see Kisakürek et al., 1983) it is clear that the neotropical and African species groups are independent and "natural" groups which must have originated separately from the Australasian center of the genus. Some major biosynthetic pathways of indole alkaloids in the Rubiaceae and related families depicted in Figure 13 demonstrate the broad representation of widespread corynanthean (C) and vallesiachotaman (V) types (e.g., C3a: corynantheine, etc.; C4a: ajmalacine, etc.; C4b: ourouparine; C4d: rhynchophylline, etc.; C5b: mitraphylline, etc.; V4: angustine, etc.) in the Australasian species of *Uncaria*, as contrasted with their reduction or even loss in the neotropical and African species. In the latter, a rare skeleton rearrangement has led to the origin of a specialized C5t type (dihydrocorynantheine-pseudoindoxyl).

From the older literature (e.g., Schumann, 1891), rather close affinities among neo- and paleotropical genera of the **Cinchoneae** had appeared likely. More recent data on seed anatomy (Lorenz-Liburnau, 1986) and alkaloids (Kisakürek et al., 1983) do not support such links. The neotropical genera *Cinchona, Remija*, and *Ladenbergia* have flattened seeds with undivided wings, a centrally located hilum and similar ad- and abaxial testa cells; a secondary chromosome base of $x = 17$; and alkaloids of the cinchonamine (C4g) and quinamine (C5l) type. The latter are absent in the African genera *Corynanthe* and *Pausinystalia*, where they are replaced by indole alkaloids of the C3a, C4a, C4b, and C4d type (cf. Fig. 13). No indole alkaloids have been found so far in the African-Asian genus *Hymenodictyon* with a $2x$–$4x$–$6x$ polyploid series on $x = 11$. Seeds of the three paleotropical genera of Cin-

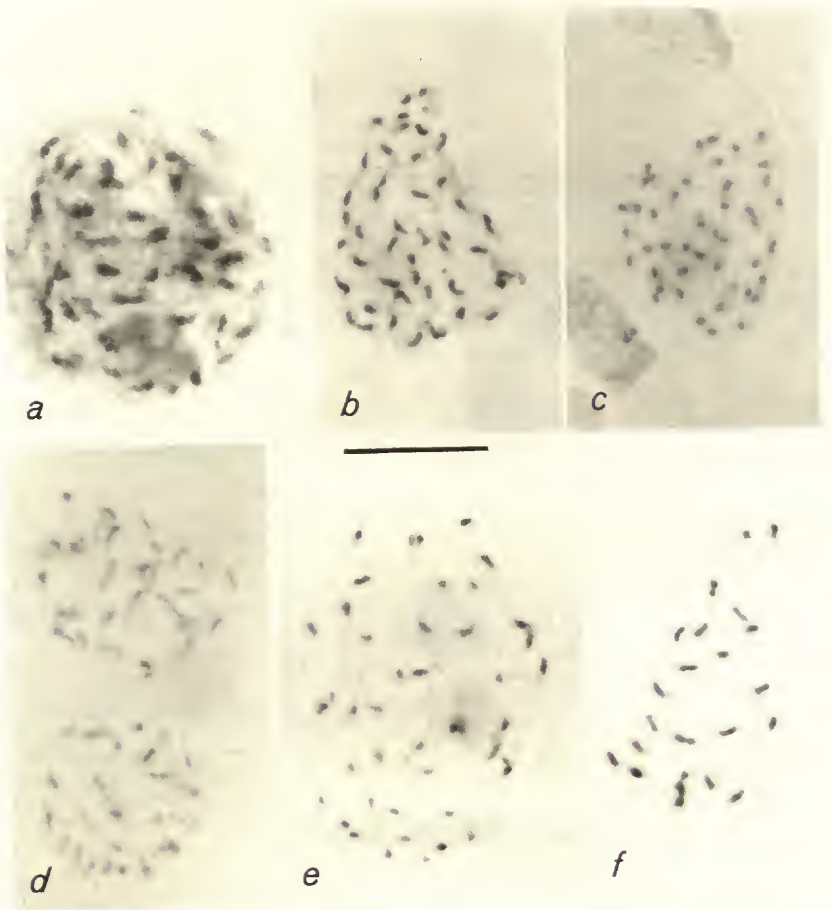

FIGURE 12. Mitotic chromosomes of Rubiaceae—Naucleeae sensu lato (a–c) and Rubiaceae—Cinchoneae (d–f).—a. *Uncaria africana* subsp. *lacus-victoriae* (Africa), $2n = 44$.—b. *Adina pilulifera* (East Africa), $2n = 44$.—c. *Cephalanthus occidentalis* (North America), $2n = 44$.—d. *Cinchona* spec. (South America, cult. Africa), $2n = 34$.—e. *Hymenodictyon floribundum* (Africa), $2n = 44$.—f. *Crossopteryx febrifuga* (Africa), $2n = 22$. Feulgen staining; scale 10 μm. (From Kiehn, 1985, 1986b.)

choneae mentioned above have wings with a basal cleft reaching the marginally situated hilum, and the testa cells are different on the ad- and abaxial sides of the flattened seed. These data suggest that relationships between these two neo- and paleotropical groups of Cinchoneae are distant.

CONCLUSIONS

More advanced methods of systematic botany not only can help to make our taxonomic groupings of tropical trees more "natural" but also can contribute to a better understanding of their phytogeographical affinities. In respect to the African dendroflora, these affinities are complex and range from relatively recent links, resulting from long-distance dispersal, to quite ancient and possibly plate tectonic conditioned patterns. Space and time do not permit me to relate in detail the examples presented with the current discussion on the relationships and origins of the African dendroflora (see e.g., Hepper, 1965; Thorne, 1972, 1973; Raven & Axelrod, 1974; Axelrod & Raven, 1978; Werger, 1978; White, 1983a, 1983b; Thenius, 1984; Kubitzki, 1985), but let me conclude with a short review.

For the American → African type of disjunction, I have discussed examples from *Annona*, the *Annona* tribe, the *Hernandia ovigera* group, the Siparunaceae, *Zanthoxylum*, and *Cochlospermum*. For the reverse African → American

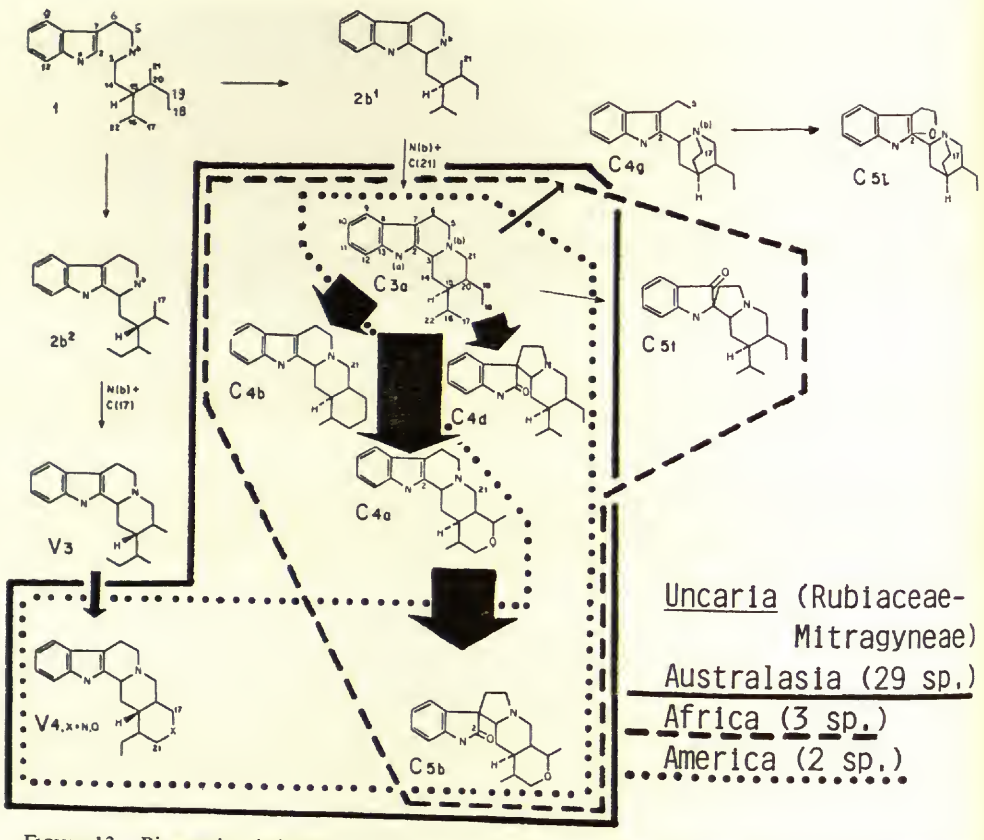

FIGURE 13. Biogenetic relationships of indole alkaloids (skeletal types C, V) with a C_9- or C_{10}-monoterpene moiety and their occurrence among species of *Uncaria* (Rubiaceae) in Australasia (center of diversity, 29 spp.), Africa (3 spp.), and America (2 spp.). (Data from Kisakürek et al., 1983.)

relationship, cases were presented from the *Annona* subfamily, the *Hexalobus* and *Anaxagorea* tribes, and from *Tetracera*. In other families like the Rutaceae or the Rubiaceae-Cinchoneae, the Atlantic Ocean apparently has been a much more effective barrier to dispersal. Among the links between Africa and Asia/Australasia, there is an apparently older and more southern (Gondwanaland?) type; it includes groups mostly centered in Australasia today, depauperate towards the West, and often reaching the Malagasy region only. Examples come from the Winteraceae, *Ascarina*, the Monimiaceae sensu stricto, the *Evodia* group of Rutaceae, *Dillenia*, and *Hibbertia*. Fossils of Winteraceae, Atherospermataceae, and *Ascarina* demonstrate the formerly more extensive area of such groups in Africa, etc. More northern connections between Africa and Asia evidently have been available until much more recently as demonstrated by examples, both of the Asian → African type (the *Goniothalamus* group, *Artabotrys*, Hernandiaceae, the *Acronychia* group, *Aurantioideae, Cephalanthus, Mitragyna*, and *Uncaria*) and of the African → Asian type (*Polyalthia, Zanthoxylum*, and *Tetracera*). Other phytogeographical links mentioned have been from tropical African groups towards the Cape flora (Diosmeae) and towards Europe and the northern hemisphere (Atherospermataceae and *Fagaropsis/Phellodendron*).

Many of these more general phytogeographical conclusions are still hypothetical, but I am optimistic that further multidisciplinary and synthetic research will improve our understanding of the origin and intercontinental affinities of the African dendroflora.

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LEAF ANATOMY AND SYSTEMATICS OF *PANICUM* (POACEAE: PANICOIDEAE) IN SOUTHERN AFRICA

ROGER P. ELLIS[1]

ABSTRACT

In this study the genus *Panicum* in southern Africa has been divided into five groups on the basis of photosynthetic leaf anatomy. These groups correspond to the different photosynthetic pathways known in the Poaceae—non-Kranz or C_3, C_3/C_4 intermediate, and Kranz or C_4, which is further subdivided into NADP-me, PEP-ck, and NAD-me types. These groups can be distinguished anatomically, and individual species are assigned to them using mesophyll and bundle sheath characteristics. Once constituted, each grouping was evaluated using all anatomical characters of the leaf blade in transverse section and abaxial epidermis, as well as morphology. By this means discrete groups of species that share similar anatomical and morphological characteristics were recognized within each photosynthetic group. The relationships of these species and species groups are discussed with reference to other *Panicum* species and panicoid genera. Many of the anatomical entities recognized showed very close resemblances to other panicoid genera, and a taxonomic reassessment of *Panicum* should take this evidence into account. The phylogenetic significance attached to photosynthetic characteristics by Brown (1977) seems to be corroborated by this study, which examined nonphotosynthetic anatomy, morphology, and ecology in addition to the Kranz and non-Kranz characteristics.

RÉSUMÉ

Dans cette étude le genre *Panicum* du sud de l'afrique a été divisé en cinq groupes sur la base de l'anatomie foliaire photosynthétique. Ces groupes correspondent aux differents types de photosynthèse connus chez les Poacées: non-Kranz ou C_3, C_3/C_4, intermediaire, et Kranz ou C_4, qui est subdivisé en trois types (NADP-me, PEP-ck, NAD-me). On peut distinguer ces groupes anatomiquement et des espèces individuelles leur sont associées en utilisant les caracteristiques du mésophylle et de la gaine vasculaire. Chaque groupement a été evalué sur la base de tous les caractères anatomiques de la lame foliaire en coupe transversale et en épiderme abaxiale, aussi bien que la morphologie. Ainsi, on a reconnu à l'interieur de chaque groupe photosynthétique des groupes nets d'espèces qui ont des caractères anatomiques et morphologiques en commun. Les auteurs discutent les relations de ces espèces et groupes d'espèces en se référant à d'autres espèces de *Panicum* et d'autres genres des Panicoïdées. Parmi les entités reconnues nombre étaient celles qui ressemblaient de très près à d'autres genres de Panicoïdées, et on devrait tenir compte de ces données pour une réévaluation taxonomique de *Panicum*. Cette étude, qui examine l'anatomie non-photosynthétique, la morphologie, et l'écologie de même que les caractères Kranz et non-Kranz, semble confirmer l'importance phylogénique que Brown (1977) accordait aux caractères photosynthétiques.

That the five subfamilies of the Poaceae represent natural groups is strongly supported by recent evidence documenting the taxonomic distribution of the C_3 and C_4 photosynthetic pathways in these subfamilies (Brown, 1977; Ellis, 1977; Waller & Lewis, 1979). Only the C_3 pathway or Calvin Cycle has been reported in the Bambusoideae and Pooideae, with the Arundinoideae being C_3 except for a few genera which have the C_4 pathway. In the Chloridoideae only the C_4 pathway is found with one possible exception (Ellis, 1984). In the Panicoideae the C_4 pathway and Kranz anatomy predominates, and it is only the tribe Paniceae which contains several C_3 representatives. The genera, tribes, and subfamilies of the Poaceae are, therefore, remarkably uniform for photosynthetic pathway and, consequently, great taxonomic significance is nowadays attached to these characteristics by most agrostologists.

The genus *Panicum* L. is unique in the Poaceae in that it includes species exhibiting all five photosynthetic types known in the Poaceae. Included in *Panicum* are C_3 and C_4 species as well as the three biochemical variants of C_4 photosynthesis, NADP-me, PEP-ck, and NAD-me types (Brown, 1977). In addition, some species are intermediate between the C_3 and C_4 pathways. All these various photosynthetic types can be distinguished anatomically by whether or not they exhibit Kranz anatomy. If Kranz, then the position of the chloroplasts in the Kranz cells and whether

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a single or a double bundle sheath surrounds the first order vascular bundles is significant (Brown, 1977; Ellis, 1977; Hattersley & Browning, 1981).

For this reason the taxonomy, anatomy, and physiology of *Panicum* has received considerable attention in recent years. Brown (1977) examined the occurrence of the Kranz syndrome in the Poaceae and paid particular attention to *Panicum* and the Paniceae. As a result of this broadly based study, he modified the subgeneric groups within *Panicum* so that each was homogeneous for anatomical and photosynthetic type. The creation of these uniform anatomical groups sometimes involved segregation of species at both the subgeneric and generic levels. These decisions were based on the assumption that leaf anatomical characters, particularly those of the Kranz syndrome, are more fundamental and conservative than the morphological characters traditionally used in the Paniceae.

Brown's (1977) suggestions have not yet been generally accepted by many taxonomists, nor have they been formally incorporated into the classification of the genus. It is the purpose of the present study to evaluate Brown's findings using the southern African species from a larger sample of anatomical specimens and to incorporate nonphotosynthetic anatomical characters as well. In addition, because of the heterogeneity of *Panicum* and its interrelationships with other panicoid genera, it is impossible and unwise to comment on the genus without adequate reference to the whole of the Paniceae. Thus, all other southern African panicoid grasses were included in the study sample. Therefore, the genus was subdivided using the photosynthetic anatomy of the Kranz syndrome and then each of these groups was evaluated using all the anatomical characteristics of the leaf blade and epidermis. In this way an attempt has been made to assess the taxonomic relevance of the Kranz syndrome in *Panicum* and the Paniceae and, by implication, in the taxonomy of the family as well. These anatomical studies have undoubtedly emphasized the fact that *Panicum* cannot be studied in isolation, and this must be borne in mind for any taxonomic revision.

Materials and Methods

Field collections of *Panicum* specimens were made throughout southern Africa between 1970 and 1985. Herbarium voucher specimens were prepared for identification purposes and were verified by the South African National Herbarium (PRE), where they are housed. These voucher specimens and their collection localities are cited where relevant in the text according to the system of Edwards & Leistner (1971).

Segments of fresh leaf blade material were removed in the field and immediately fixed in FAA (Johansen, 1940). Transverse sections, 10 μm thick, were prepared after desilicification in 30% hydrofluoric acid (Breakwell, 1914), dehydration using the method of Feder & O'Brien (1968) and infiltration and embedding in Tissue Prep (Fischer Scientific). The sections were stained in safranin and fast green (Johansen, 1940). The manual scraping method of Metcalfe (1960) was used to prepare epidermal scrapes of the abaxial epidermis. These were stained in safranin. The anatomy was recorded photographically.

Nearly 200 specimens of *Panicum* were collected and prepared by these methods. This sample includes 30 of the 40 species that occur in the Flora of Southern Africa region (Smook & Gibbs Russell, 1984). Notably, 20% of the sample could only be identified to genus, indicating that there are still difficulties with the morphological delimitation of taxa. However, it was possible to assign all unidentified specimens to a particular group using only anatomical criteria.

After recording and describing the leaf anatomy of these 30 species of *Panicum*, anatomical comparisons were made with over 800 southern African grass species from a total collection of 5,000 specimens, all collected and prepared by the same methods. By this means, the leaf anatomy of the *Panicum* species could be adequately compared and contrasted with a representative sample, particularly of the Paniceae.

Results and Conclusions

The *Panicum* specimens examined in this study were assigned to four major anatomical groups (Fig. 1) on the basis of the characteristic leaf anatomy that distinguishes the four different photosynthetic types known in the Poaceae (Brown, 1977; Ellis, 1977; Hattersley & Browning, 1981). The diagnostic anatomical characteristics correlated with each of the photosynthetic types were therefore used to assign each specimen to a group representing a particular photosynthetic pathway (C_3; C_4 PEP-ck; C_4 NAD-me; C_4 NADP-me; and an additional C_3/C_4 intermediate group).

The leaf anatomy of each group was further

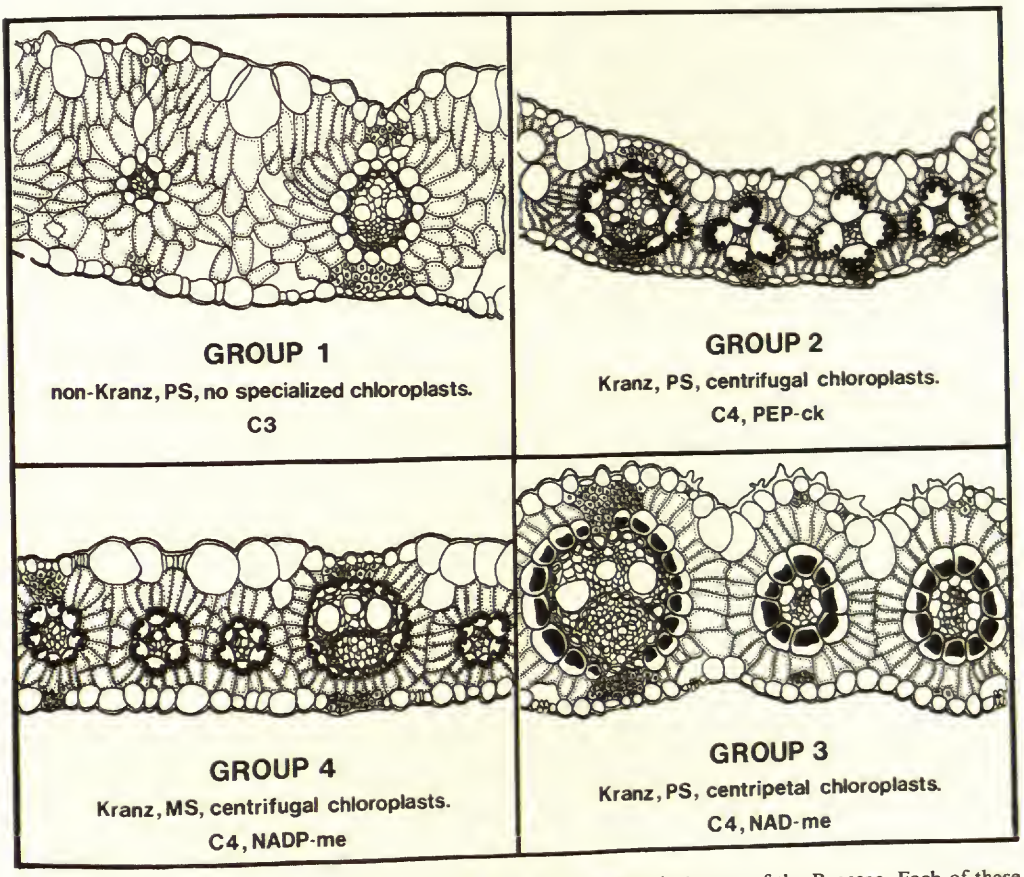

FIGURE 1. Diagrammatic representation of the four major anatomical types of the Poaceae. Each of these anatomical types is associated with a different pathway of photosynthesis, either C_3 or one of the three biochemical variants of C_4 photosynthesis. *Panicum* is unique in that all four anatomical and photosynthetic groups occur in this single genus.

evaluated by examination of all the anatomical characters of the leaf blade in transverse section (Ellis, 1976) and epidermis (Ellis, 1979). Thus, equal emphasis was given to all leaf blade anatomical characters in an attempt to establish whether the major groups based on photosynthetic anatomy also represent uniform, homogeneous groups based on overall leaf anatomy. In this way the taxonomic significance of the various photosynthetic pathways in *Panicum* and the Paniceae was further assessed prior to a comprehensive revision of the genus. If it can be shown that the photosynthetic types also represent natural, evolutionary lines, then the taxonomy of the genus should be greatly improved and simplified by incorporation of this structural and functional evidence.

The four groups will be discussed separately, each being further divided into subgroups of species sharing similar anatomy. The leaf anatomy and possible taxonomic relationships of the constituent species will be individually described and discussed.

GROUP 1

The non-Kranz *Panicum* species found in southern Africa do not form a uniform, coherent anatomical group. At least three, and possibly four, discrete anatomical entities can be identified and defined.

The first two groups include the majority of the South African C_3 *Panicum* and panicoid species (Table 1). These two categories include

TABLE 1. Relationships of non-Kranz, C_3 *Panicum* species.

Group 1	Non-Kranz, C_3, *Panicum* Species	Non-Kranz, C_3, Panicoid Taxa
1a	*P. laticomum* *P. monticola* *P. heterostachyum* *P. parvifolium* *P. aequinerve* *P. hymeniochilum*	*Oplismenus* *Pseudechinolaena* *Sacciolepis curvata*
1b	*P.* spp. aff. *hymeniochilum* *P. brevifolium*	*Acroceras* *Sacciolepis*
1c	*P. ecklonii*	
1d	*P. natalense*	

all the shade-loving, herbaceous, procumbent species with lanceolate leaves. These species share a distinctive leaf anatomy, both in transection and epidermal structure, which distinguishes them from other panicoid grasses. They also differ substantially from the other major groups of C_3 grasses—the pooid, arundinoid, and bambusoid types. However, they do superficially resemble the centhostecoid grasses, possibly an example of structural convergence in response to similar shady habitats.

The remaining two anatomical groups of C_3 *Panicum* species each only contain a single species (Table 1). These are caespitose perennials with linear, basal leaves found in full sunlight in open grassland communities. In leaf anatomy, particularly epidermal cell structure and arrangement, they differ greatly from the shade *Panicum* groups. These two groups appear to be isolated, with no close relatives in southern Africa.

GROUP 1a

This is a large group and includes either loosely tufted annuals or perennials with slender, weak, branching culms that creep, ramble or climb in the shaded ground layer of evergreen forest or scrub undergrowth. They are procumbent herbaceous plants, usually rooting at the nodes. The adventitious roots are often produced above the soil surface, the entire plant being aerially supported by this means. The leaf blades are expanded, lanceolate or ovate, soft and thin. Some species occur in less shady, more open but wet habitats and tend to have thicker leaves.

Anatomical characteristics. Anatomically this group is remarkably uniform in leaf structure. It is also distinct from most other Paniceae, both in epidermal structure and the leaf in transverse section (Fig. 2a–f). Representatives of this group possess the following anatomical characteristics:

(a) Leaves thin, 75–100 μm thick, with only 2–5 layers of mesophyll cells (Fig. 2a, c, e).

(b) Midrib conspicuous, consisting of a single median vascular bundle with prominent adaxial, and less pronounced abaxial, projections.

(c) Mesophyll arrangement is distinctive. The adaxially located chlorenchyma cells which adjoin the vascular bundles opposite the xylem tissue exhibit a very conspicuous radiate arrangement. The adaxially located chlorenchyma cells situated between the vascular bundles and below the bulliform cells are palisadelike in their arrangement. The chlorenchyma cells located nearer the abaxial surface of the lamina are irregularly arranged and large intercellular air spaces are present. The radiating cells are of the long, narrow type found in *Isachne* (Metcalfe, 1960), but the nonradiating, lower cells are shorter and irregular in shape and may even be stellate branching cells (Fig. 2a, c, e).

(d) There are always many more than four chlorenchyma cells between successive vascular bundle sheaths (8–15). The vascular bundles are consequently widely spaced and are at least 200 μm apart (Fig. 2a, c). This maximum lateral cell count is a reliable criterion for distinguishing between Kranz and non-Kranz in grasses (Hattersley & Watson, 1975) and confirms that all these species are C_3.

(e) The bundle sheaths are double with the outer sheath entire, without specialized chloroplasts but with the cell walls distinctly thicker than the walls of the chlorenchyma cells. In this respect these species differ from the pooid C_3 grasses. Kranz cells are, nevertheless, absent from all these species and many of them have been shown to be C_3 by nonanatomical means (Brown, 1977).

(f) The intercostal long cell shape is another feature that is characteristic of this group. These cells are rectangular with very sinuous cell walls in which the undulations are regular, deep and U-shaped (Fig. 2f). All the intercostal long cells are uniform in size and shape, are nucleate, and are not separated by short cells. Sometimes the long cells may be shorter and ± cubical in shape without marked undulations (Fig. 2b, d). Species exhibiting this type of long cell structure are not shade loving and their leaves are also much thicker in transection (Fig. 2e).

(g) Silica bodies are dumbbell-shaped (Fig. 2d) to angular cross-shaped (Fig. 2b). The costal zones are very narrow, from 3–5 files of cells wide.

(h) A single stomatal file is present on either side of each costal zone (Fig. 2d, f) with the rest of the intercostal zone consisting of regular long cells. The stomata have low triangular to dome-shaped subsidiary cells and are separated by single interstomatal long cells.

(i) Microhairs are scattered throughout the central region of the intercostal zones. These hairs are bicellular, very thin, with tapering distal cells. The length of the basal cell is variable, either almost equal to the stomatal length (Fig. 2d) or very much shorter (Fig. 2f). The distal cell is usually much longer than the basal, but the ratio of the two cells may also be almost equal.

Included species:

Panicum laticomum Nees (Fig. 2c, d). Habitat and growth form typical of this group of forest *Panicum* species with the leaf anatomy identical to that diagnostic for this group.

TRANSVAAL. 2330: Kruger Natl. Park, Punda Milia (DB), *Ellis 3231*.—2528: Pretoria, cultivated (CA), *Ellis 1919*. NATAL. 2732: Lake St. Lucia, False Bay (CD), *Ellis 3643*.—2832: Lake St. Lucia, estuary (AD), *Ellis 3418, 4499*.—2931: Durban (CC), *Ellis 4426*.

Panicum monticola Hook. f. Conforms very closely in anatomical structure, vegetative morphology and habitat requirements to that typical of this group.

TRANSVAAL. 2329: Tzaneen Dist. (DD), *Ellis 1867, 1869*.

Panicum heterostachyum Hack. A small, soft, erect, tufted annual from shady places beneath large woodland trees. It is not a creeping perennial as are the other taxa from this group. The leaf anatomy conforms closely to that described for this group, and it undoubtedly belongs here.

S.W.A. 1724: Caprivi Zipfel (CB), *Ellis 3724, 3725*. TRANSVAAL. 2330: Kruger Natl. Park, Punda Milia (DB), *Ellis 1923*.

Panicum parvifolium Lam. (Fig. 2a, b). This species is found in swamps and marshes, where it ascends and climbs on taller grasses and sedges. In these situations it is rooted in saturated peaty soils but the leaves may be exposed to direct sunlight. The leaf anatomy also differs somewhat from the standard type of this group, the midrib being absent and the intercostal long cells cubical without very sinuous walls (Fig. 2b). This species is nevertheless retained in this group together with some others that also diverge in anatomical structure and ecological requirements from that which defines and distinguishes the group from most other panicoid grasses.

TRANSVAAL. 2528: Pretoria, cultivated (CA), *Ellis 412, 1816*. NATAL. 2732: Tongaland, Sordwana Bay (DA), *Ellis 3570*.—2831: Zululand, Ngoye Forest (DC), *Ellis 3394*.

Panicum aequinerve Nees (Fig. 2e, f). This species exhibits a wider ecological tolerance than any of the above. It is found in deep forest shade but also occurs on forest margins and even in open grassland situations in cool, damp, mistbelt regions. A large anatomical sample has been examined, incorporating specimens from all these habitats. Specimens from shady habitats tend to have a developed midrib, unlike specimens from localities with more sunlight. There is also a corresponding increase in leaf thickness along this insolation gradient, with the thickest leaf (Fig. 2e) having been collected in open grassland. Care must therefore be exercised in relating this anatomical category only to genetic causes, as it may merely reflect environmental differences. Nevertheless, all specimens of *P. aequinerve* conform closely to the anatomical diagnosis of this group and obviously belong here.

TRANSVAAL. 2330: Tzaneen Dist. (CC), *Ellis 3491*.—2430: Sabie Dist., Graskop (DD), *Ellis 4466*.—2531: Barberton Dist. (CA), *Ellis 1541*. NATAL. 2731: Vryheid Dist., Ngome (CD), *Ellis 3342, 3343*.—2829: Ca-

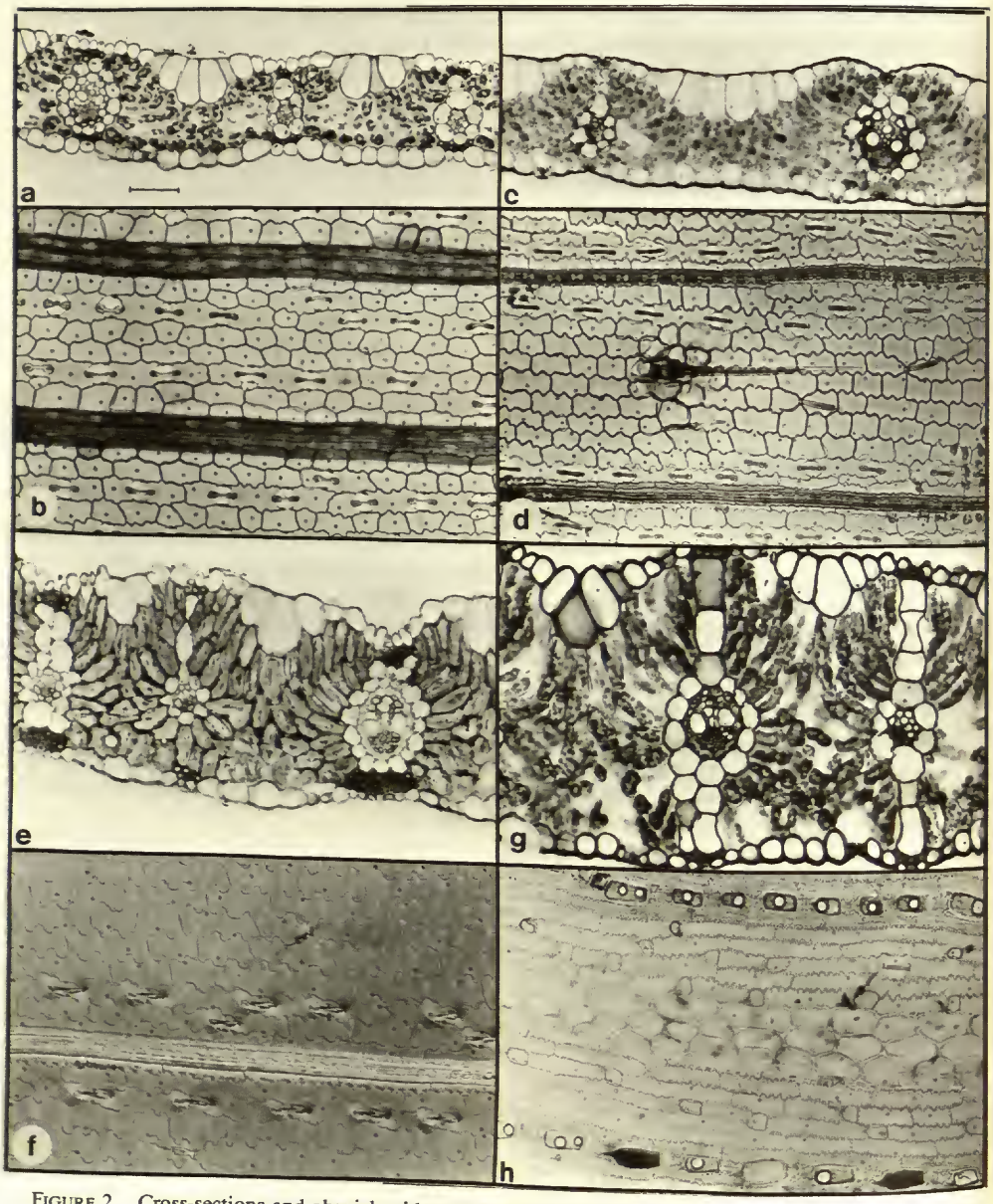

FIGURE 2. Cross-sections and abaxial epidermal scrapes of the leaf blades of the non-Kranz, C_3 *Panicum* species of Groups 1a and 1b from shady or moist habitats.—a–f. Group 1a, shade-loving forest species.—a, b. *P. parvifolium*; a, *Ellis 412* with the vascular bundles separated by more than four mesophyll cells; b, *Ellis 1816* with short intercostal long cells without sinuous walls.—c, d. *P. laticomum, Ellis 191*; c, palisadelike adaxial chlorenchyma; d, note macro- and microhairs.—e, f. *P. aequinerve*; e, *Ellis 2104,* relatively thick leaf from sunny locality; f, *Ellis 1541,* typical epidermal cell pattern of forest panicoid grasses.—g, h. Group 1b, herbaceous creeping species from damp, sunny habitats, *P.* sp. aff. *hymeniochilum.*—g. *Ellis 4492,* note bundle sheath extensions, thickness of blade and distance between vascular bundles.—h. *Ellis 3403,* note silicified prickles. Scale = 50 μm.

thedral Peak (CC), *Ellis 1453, 1457.*—2929: Underberg Dist., Donnybrook (DD), *Ellis 214.*—2930: Greytown Dist., Rietvlei (AB), *Ellis 3366*; Merthley Dam (BA), *Ellis 3370*; Pietermaritzburg (CB), *Ellis 4419.*—3030: Port Shepstone Dist. (CD), *Ellis 1470.* CAPE. 3227: Amatola Mts., Hogsback (CA), *Ellis 1476*; Komga Dist. (DB), *Ellis 283, 1101.*—3228: Haga Haga Beach (CC), *Ellis 2103, 2104.*

Panicum hymeniochilum Nees. Two distinct anatomical entities appear to be included under this name, and both differ from the diagnosis of this group. The first, a species of stream banks and marshes, has an epidermis very similar to that typical of the shade *Panicum* group. The leaf sections are thicker, and conspicuous bundle sheath extensions, adaxial ribs, and furrows are present. No midrib or keel is developed. This anatomy can be accommodated in this group, but the leaf anatomy of other specimens assigned to this taxon differs substantially. These specimens are referred to as *P.* sp. aff. *P. hymeniochilum* and are placed in the next group. It is possible that intermediates will be found between these two groups, particularly in tropical Africa, but they are separated here in order to emphasize their differences. This second taxon is only known from true swamps in northern Natal, whereas true *P. hymeniochilum* occurs in more temperate highveld grasslands. Comparison of Figure 2g, h with the rest of the figure illustrates the anatomical differences between these two taxa.

TRANSVAAL. 2530: Nelspruit Dist. (BD), *Ellis 1560*; Barberton Dist. (DC), *Ellis 465.*—2630: Piet Retief Dist., Amsterdam (DA), *Ellis 1523.* NATAL. 2830: Tugela Valley (DD), *Ellis 3373.*—3030: Port Shepstone Dist. (DA), *Ellis 3778.*

Discussion. This type of leaf anatomy is therefore consistent for a number of panicoid grasses inhabiting the shady ground layer of forests. However, some species with this type of anatomy occupy sunnier localities on forest margins or in adjacent marshes. This change in habitat is accompanied by certain anatomical changes such as thicker leaves with the vascular bundles located much closer together (Fig. 2e) and the intercostal long cell walls less sinuous (Fig. 2b). Nevertheless, these species can still be accommodated within this very discrete anatomical grouping.

In leaf anatomy, vegetative morphology, and ecological requirements this group of *Panicum* species forms a remarkably homogeneous group. Other C_3 *Panicum* species can be assigned to this group on the basis of published anatomical descriptions and illustrations. Examples are *P. clandestinum* L. (Metcalfe, 1960; Ellis, unpubl.), *P. trichanthum* Nees (Ralph, 1983; Wilson et al., 1983), and *P. bisulcatum* (Takeda & Fukuyama, 1971). These species are all herbaceous plants with lanceolate leaf blades from shady habitats. Undoubtedly many more *Panicum* species belong here and it should be possible to assign them on the basis of morphology and ecology. Possibilities are *P. pusillum* Hook. f., *P. delicatulum* Fig. & De Not., *P. comorense* Mez., *P. robynsii* A. Camus, *P. nudiflorum* Renv., *P. hochstetteri* Steud., *P. calvum* Stapf, *P. malapense* Pilg., *P. issongense* Pilg., *P. chionachne* Mez., *P. trichoides* Sw., *P. mueense* Vanderyst, *P. mitopus* K. Schum., and *P. pleianthum* Peter from tropical Africa (Clayton & Renvoize, 1982).

In southern Africa there are several other panicoid grasses with similar morphology and ecology to these *Panicum* species (Table 1). These are also C_3 grasses (Ellis, 1974a, 1977; Brown, 1977) and their leaf anatomy is identical to that characteristic of this group. Examples are *Oplismenus burmannii* (Retz.) Beauv., *O. hirtellus* (L.) Beauv., *Pseudechinolaena polystachya* (H.B.K.) Stapf, and *Sacciolepis curvata* (L.) Chase. Australian species that conform anatomically to this structure include *Pseudechinolaena polystachya* and *Sacciolepis indica* (Clifford & Watson, 1977). The relationships of these C_3 panicoid grasses and the *Panicum* species of Group 1a (and possibly Group 1b) appear to be much closer than to any of the *Panicum* species of the C_4 groups.

Other African genera which may belong to this assemblage, as evidenced by growth form and habitat requirements, are *Cyrtococcum*, *Chloachne*, *Poecilostachys*, and *Echinolaena*. The leaf anatomy and epidermal structure of *Chloachne oplismenoides* (Hack.) Stapf (Jacques-Félix, 1958, 1962) closely resembles that described for this group. All species of *Lasiacis*, from the New World, belong to this group on the basis of leaf anatomy (both epidermis and transection structure) and all are also shade species of forests (Davidse, 1978). In *Lasiacis* there is also a certain degree of variation in growth form from herbaceous, procumbent to woody and erect species, and this is accompanied by anatomical trends similar to those described for *P. aequinerve*.

It therefore appears as if all panicoid grasses with this type of growth form and habitat can be predicted to exhibit this type of anatomy. *Microstegium nudum* (Trin.) A. Camus is the most notable exception, being Kranz yet resembling the taxa of this group in vegetative morphology and habitat requirements. However, this grass is an andropogonoid, all of which are C_4 (Ellis, 1977). Therefore, this argument strictly applies only to eu-panicoid taxa. *Brachiaria chusqueoides* (Hack.) Clayton and *Panicum obumbratum* Stapf are two eu-panicoid species that may not conform to this prediction, as they superficially resemble this group in vegetative morphology and habitat requirements yet are C_4 (Ellis, 1977).

Panicum, as presently constituted, thus seems to be a heterogeneous and almost certainly polyphyletic genus with relationships to many other eu-panicoid genera. The present study indicates that all the shade-loving taxa with a creeping habit and lanceolate leaves comprise a very uniform and distinct anatomical group. The possibility that they also form a coherent suprageneric taxon warrants consideration.

GROUP 1b

This group is very close to the above in vegetative morphology and ecological requirements. It also comprises creeping, much branched, herbaceous grasses usually climbing over other vegetation and not procumbent on the ground. These grasses are more hydrophytic, even floating in open water, and definitely prefer greater insolation than members of the previous group. Groups 1a and 1b probably intergrade (Table 1) but are artificially kept separate here because in southern Africa no anatomical intermediates have yet been found.

Anatomical characteristics. Species of this group differ somewhat in leaf anatomy from Group 1a, yet there are shared attributes which serve to stress the close relationships between the two groups. Many of the specimens and species of Group 1a differ slightly from the anatomical diagnosis of the group and possess one or two characteristics of Group 1b. Their separation is therefore somewhat subjective and artificial. Group 1b differs anatomically from Group 1a in the following ways:

(a) Leaves much thicker, up to 200 μm thick (Fig. 2g).

(b) No distinctive keels are present but instead the median part of the blade is thickest.

(c) The distinctive mesophyll arrangement of Group 1a is modified slightly. The palisadelike chlorenchyma is not as well developed because the interveinal distances are not as great, as a comparison of Figure 2c and g shows.

(d) The vascular bundles are closer together (less than 100 μm apart) and only about four mesophyll cells separate adjacent bundle sheaths (Fig. 2g).

(e) All vascular bundles are linked to the adaxial and abaxial epidermis by means of prominent, uniseriate, colorless sheath extensions (Fig. 2g).

(f) The intercostal zone cell structure and arrangement is not consistent across intercostal zones and differs substantially from the configuration in Group 1a (Fig. 2h).

(g) The silica bodies are also irregularly dumbbell- to cross-shaped.

(h) Stomata are rare and occur only irregularly on the abaxial surface.

(i) Microhair structure is much the same as in the previous group but their occurrence is less regular.

(j) Silicified hooks and prickles are often present (Fig. 2h).

Included species:

Panicum sp. aff. *P. hymeniochilum* Nees (Fig. 2g, h). This taxon of uncertain identity includes several collections from the Lake St. Lucia and Tongaland region of Natal. All specimens are genuine hydrophytes found floating in water up to 1.5 m deep. Their anatomy and morphology is distinct from *P. hymeniochilum.* They warrant separate specific status.

NATAL. 2732: Tongaland, Sordwana Bay (BA), *Ellis 3571.*—2832: Lake St. Lucia, Lake Bangazi (BA), *Ellis 3403, 4492.*

Panicum brevifolium L. A creeping annual from damp places on forest margins, usually in sunny openings. This species is not a hydrophyte but may be able to respond to and survive inundation. It differs considerably from the forest *Panicum* species in leaf anatomy and closely resembles that illustrated in Figure 2g and h. The illustrations of Jacques-Félix (1958) for this species are typical of forest *Panicum* species and there obviously is a problem with the true identity of his collection.

NATAL. 2632: Tongaland, Kosi Bay (DD), *Ellis 4076.*

Discussion. Many specimens of Group 1a tended towards this type of anatomical structure. Figure 2e illustrates a *Panicum aequinerve* specimen from a full sunlight situation that has a leaf much thicker than normal for Group 1a and that resembles the condition found in Group 1b. However, the epidermal pattern of this specimen is typical of Group 1a. No specimen placed in Group 1b has the characteristic epidermal pattern of Group 1a.

This small yet distinct group in southern Africa may include some tropical African *Panicum* species. Possibilities are *P. pole-evansii* C. E. Hubb., *P. nigromarginatum* Robyns and *P. adenophorum* K. Schum. (Clayton & Renvoize, 1982).

In southern Africa this group appears to be somewhat isolated (Table 1). Only *Acroceras macrum* Stapf bears a close anatomical resemblance to it (Ellis, 1974a, 1977). Members of this group, however, resemble the hygrophilous *Sacciolepis* species in some anatomical aspects. This may only indicate anatomical convergence in response to similar environmental conditions and not necessarily phylogenetic relationships. In this context it is significant that *S. curvata,* a shade-loving forest species, differs greatly in leaf anatomy and resembles Group 1a in anatomy (Table 1). The hygrophilous *Sacciolepis* species, however, agree closely in leaf anatomy with these hygrophilous C_3 *Panicum* species.

Nevertheless, even if Groups 1a and 1b are artificial anatomical groupings, not justifying taxonomic recognition, their constituent species are undoubtedly more closely related to each other than they are to any of the *Panicum* species of the other three main anatomical groups. They are, therefore, probably better classified together with genera such as *Sacciolepis, Oplismenus, Pseudechinolaena,* and others than with any of the C_4 *Panicum* species.

GROUP 1c

This group contains only *Panicum ecklonii* Nees, a densely tufted perennial. The leaves are basal, expanded and usually densely hairy. The hairs are tubercle-based and fine or occasionally gland-tipped. *Panicum ecklonii* is found in open grassland, mainly highland sourveld, and is particularly frequent in areas subjected to burning (Chippindall, 1955).

Anatomical characteristics. Panicum ecklonii has non-Kranz leaf anatomy that resembles Group 1b more than that of the shade *Panicum* Group 1a. It differs anatomically from Groups 1a and 1b in the following respects:

(a) Leaves up to 200 μm thick (Fig. 3a).

(b) No clearly distinguishable midrib is developed and the median part of the blade is thickest. Shallow, but well-defined, adaxial ribs and furrows are present (Ellis, 1974a).

(c) The diagnostic mesophyll arrangement of Group 1a is considerably modified, and palisadelike cells are absent. This is because the vascular bundles are closer together. The chlorenchyma is nevertheless of the radiate type, particularly those cells adjacent to the xylem tissue (Ellis, 1977).

(d) The vascular bundles are less than 120 μm apart and only 4–6 chlorenchyma cells separate successive bundles (Fig. 3a).

(e) All vascular bundles are linked to the sclerenchyma strands of both the upper and lower leaf surfaces by prominent multiseriate bundle sheath extensions (Fig. 3a). Bundle sheath extensions are lacking in the shade *Panicum* species of Group 1a but uniseriate extensions are characteristic of Group 1b.

(f) The intercostal cell structure and arrangement bears little resemblance to that typical of Group 1a. The zones themselves are much narrower and the long cells are more elongate and have less prominent undulations. The typical jigsawlike appearance of these cells in the forest *Panicum* group is not found in *P. ecklonii* (Fig. 3b).

(g) The silica bodies are regular dumbbell-shaped, alternating with short cells along individual files of costal cells. The costal zones are 5–7 cells wide.

(h) Each intercostal zone has two files of stomata, a single row adjacent to each costal zone. Subsidiary cells are low dome-shaped (Fig. 3b).

(i) Microhair structure differs substantially from that in the previous two groups. These hairs are longer (50–65 μm) and wider (up to 25 μm) with the two cells almost equal in length and with comparable wall thickness. The distal cell tapers to a definite point (Fig. 3b).

(j) Silicified hooks, prickles and long cells found in Group 1b are absent.

(k) Macrohairs are common and differ from those of Group 1a. Unicellular, pointed cushion hairs as well as multicellular, glandular tipped

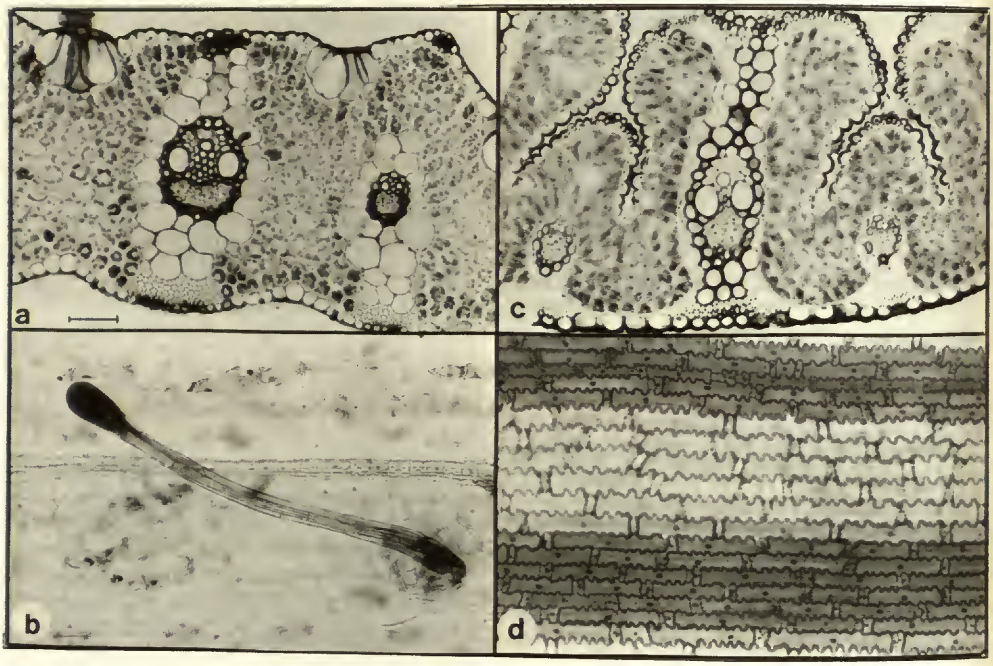

FIGURE 3. Leaf blade anatomy of the open grassland C_3 *Panicum* species of Groups 1c and 1d.—a, b. Group 1c, *P. ecklonii*; a, *Ellis 53* with multiseriate bundle sheath extensions and bundles close together; b, *Ellis 4319*, note multicellular glandular macrohair and large microhairs.—c, d. Group 1d, *P. natalense*; c, *Ellis 223*, note adaxial ribs and furrows and thin walls of outer bundle sheath cells; d, *Ellis 1442*, note absence of stomata and microhairs. Scale = 50 μm.

hairs occur (Fig. 3b). The latter are unique in the Poaceae (Kabuye & Wood, 1969) and are only known in representatives of this anatomical grouping.

Included species:

Panicum ecklonii Nees (Fig. 3a, b). This is the only species from southern Africa included in this group. Several tropical African *Panicum* species that possess multicellular clavellate hairs may also belong here.

TRANSVAAL. 2430: Tvl. Drakensberg, Penge (AD), *Ellis 2815, 2816, 2827*; Graskop (DD), *Ellis 4312, 4313, 4319*.—2630: Amsterdam (DA), *Ellis 1856*. NATAL. 2729: Majuba Pass (DB), *Ellis 30a*.—2829: Cathedral Peak (CC), *Ellis 1421, 1449*.—2929: Underberg (BD), *Ellis 53*; Giants Castle (AB), *Scotcher s.n.*

Discussion. Panicum ecklonii differs little from members of Group 1b in transectional leaf anatomy. However, the epidermal structure of these two groups is distinct, particularly in possessing multicellular macrohairs and in the size of the microhairs of *Panicum ecklonii*. It shares little with the forest species of Group 1a apart from being non-Kranz.

The separation of *Panicum ecklonii* from Group 1b in particular may prove to be artificial, as these two groups may intergrade. Kabuye & Wood (1969) mention several other tropical African *Panicum* species that possess multicellular hairs. Examples are *P. adenophorum* K. Schum., *P. flacciflorum* Stapf, *P. kisantuense* Robyns, *P. lukwangulense* Pilg., and *P. snowdenii* C. E. Hubb. *Panicum adenophorum* and *P. snowdenii* have been shown to be C_3 (Brown, 1977) and the remainder are presumably also non-Kranz species, although their photosynthetic status and anatomy have yet to be determined. This small complex of species probably constitutes a discrete group of non-Kranz species all with unique multicellular hairs.

Anatomically *Panicum ecklonii* resembles the *Panicum* species of Group 1b most closely. *Panicum hymeniochilum* possesses clavellate hairs (Clayton & Renvoize, 1982) but it is not known whether these are multicellular or not. If such

hairs are found to occur in species of this group, this will support their combination. Group 1a, Group 1b, and *P. ecklonii* possibly form a continuum and it may not be appropriate to recognize three distinct taxa on morphological criteria (Table 1). The anatomical groups may simply represent the structural manifestation of an ecological cline from mesic shady habitats to drier, sunnier open grassland. Nevertheless, these three very closely related groups of *Panicum* species, together with associated non-Kranz panicoid genera, appear to warrant taxonomic recognition separate from the C_4 *Panicum* groups.

Panicum ecklonii appears to have no close relatives among the other non-Kranz panicoid genera of southern Africa. It is of interest to note that *Alloteropsis semialata* (R. Br.) Hitchc. subsp. *eckloniana* (Nees) Gibbs Russell possesses microhairs very similar to those of *P. ecklonii* and which differ considerably from those of other panicoid grasses. *Alloteropsis semialata* subsp. *eckloniana* does not possess multicellular macrohairs, however, although it is a C_3 species (Ellis, 1974b), which usually has unicellular cushion-based macrohairs. Most *P. ecklonii* specimens studied did not have multicellular hairs on the leaf blade epidermis, and in epidermal structure these two species are often difficult to distinguish. They also occupy identical grassland habitats but show no spikelet similarities at all. Little phylogenetic importance should be attached to their anatomical similarities.

GROUP 1d

Panicum natalense Hochst. is the sole South African representative of this very distinct and isolated group. It is a strongly caespitose perennial with glabrous, setaceous or rolled leaf blades. It grows in open grassland and is a typical constituent of sourveld. Chippindall (1955) stated that *P. natalense* belongs to a group well represented in tropical Africa but did not provide further details.

Anatomical characteristics. The leaf anatomy of *Panicum natalense* bears little resemblance to that of any other southern African Paniceae. It has several anatomical features unique among South African species of the tribe. Anatomical characteristics of *P. natalense* are:

(a) Leaf blade setaceous, infolded, or inrolled.

(b) Massive adaxial ribs over the first order vascular bundles and smaller ones over the third order bundles. The associated furrows are deep and cleftlike (Fig. 3c).

(c) Multiseriate bundle sheath extensions of lignified collenchyma extend to both upper and lower epidermis (Fig. 3c).

(d) Median vascular bundle indistinguishable from lateral first order bundles.

(e) Outer bundle sheath cell walls are not thicker than walls of the mesophyll cells (Fig. 3c).

(f) Mesophyll tends toward the radiate condition but less so than in other C_3 *Panicum* species (Fig. 3c).

(g) Abaxial epidermis with a thick continuous cuticle over all cells (Fig. 3c).

(h) Abaxial costal and intercostal zones comprise similar cells (Fig. 3d). Long cells are rectangular with sinuous walls with high frequency of undulations.

(i) All long cells are separated by short cells, either single or paired.

(j) No abaxial stomata are present (Fig. 3d).

(k) No abaxial epidermal appendages are present. Microhairs are noticeably absent.

(l) Silica bodies are tall and narrow, not dumbbell-shaped.

Included species:

Panicum natalense Hochst. This is the sole representative of this group.

TRANSVAAL. 2528: Pretoria, Brummeria (CA), *Ellis 417*; Pretoria, Constantia Park (CB), *Ellis 140.*—2530: Dullstroom, Steenkampsberg (AA), *Smook 4828*; Lydenburg, Long Tom Pass (BA), *Ellis 453, 460.*—2531: Barberton, Ida Doyer Nat. Res. (CC), *Ellis 376.* NATAL. 2829: Cathedral Peak (CC), *Ellis 1442.*—2929: Giants Castle (AB), *Scotcher s.n.*—3029: Kokstad (AD), *Ellis 223.*

Discussion. Panicum natalense bears little resemblance to any other South African panicoid grass, and anatomical characteristics do not even suggest a relationship with the Panicoideae. The absence of microhairs suggests pooid affinities, although it is likely that these hairs will be found to be present on the sides of the adaxial furrows. The shape of the epidermal long cells, however, is not pooid but resembles the condition often encountered in the arundinoid grasses. Leaf anatomy, therefore, does not indicate an alternative classification for this very interesting species, which appears to occupy an isolated position in the Paniceae. Further anatomical studies of species possibly related to *P. natalense* are required before a firmer opinion can be expressed

TABLE 2. Relationships of PEP-ck type *Panicum* species.

Group 2	Kranz, PS, *Panicum* Species with Centrifugal Chloroplasts		Kranz, PS, *Brachiaria* and Other Panicoid Species with Centrifugal Chloroplasts		
2a	*P. maximum* *P. infestum*	→	*B. chusqueoides* *B. obumbratum* *B. grossa*	→	*B. arrecta* *B. brizantha* *B. deflexa* *B. marlothii*
2b	*P. deustum*	←	*B. advena* *B. eruciformis* *B. malacodes* *B. schoenfelderi* *B. serrata* *Tricholaena*	←	*B. nigropedata* *B. xantholeuca* *Eriochloa* *Urochloa*
2c	*P. dregeanum* *P. fluviicola*	←	*B. dictyoneura* *B. dura* *B. humidicola* *B. subulifolia*		
2d	*P. gilvum* *P. impeditum* *P. repens* *P. schinzii* *P. subalbidum*				

concerning its affinities. Anatomy does not indicate that *P. natalense* is allied to any of the other C_3 *Panicum* groups and it may be the sole southern African representative of another, separate line of C_3 panicoid grasses.

GROUP 2

All the species included in this group have a Kranz outer bundle sheath in which the specialized chloroplasts are centrifugally arranged. These are all C_4 species probably of the PEP-ck subtype, and several of them have been biochemically typed as such (Gutiérrez et al., 1976). Most of the species placed in this category are also of doubtful taxonomic position and do not appear to be correctly referred to *Panicum* (Brown, 1977). It has been suggested that those species with transversely rugose fertile lemmas should be transferred to *Brachiaria* together with *Urochloa* and *Eriochloa* (Brown, 1977). However, this solution leaves unplaced the species without rugose lemmas but which obviously belong to this complex. In addition, some other *Panicum* species with smooth, glossy lemmas and PEP-ck type anatomy do not seem to belong to this complex centered on *Brachiaria* but instead appear to occupy an isolated position with no clear affinities with any other panicoid grasses.

The PEP-ck *Panicum* species from southern Africa thus appear to belong to two separate groups, neither of which appears to be closely allied to the C_3, NAD-me or the NADP-me groups of *Panicum*. Their relationships may lie with other panicoid genera and they have no obvious affinities with any other southern African nonpanicoid grass genera.

GROUP 2a

The species of this group have rugose upper lemmas and their classification in *Panicum* has been questioned (Gutiérrez et al., 1976; Brown, 1977). These authors suggest that they belong with genera such as *Brachiaria, Urochloa,* and *Eriochloa* and should be removed from *Panicum*. Anatomy confirms this opinion but also shows that the correlation between PEP-ck type anatomy with centrifugal chloroplasts and panicoid grasses with rugose lemmas is not perfect and that some species with smooth, shiny lemmas also belong to this complex (Table 2).

The species of this group are tropical grasses of woodland communities and appear to favor partial shade, often occurring beneath the canopies of savanna trees.

Anatomical characteristics. This group can be defined anatomically by the very unusual out-

er bundle sheath cells associated with the third order vascular bundles. The configuration of these cells is so peculiar that it is diagnostic for this group, serving to separate it from the other PEP-ck groups. This character varies, however, intergrading with the following two groups, and does not appear to provide an adequate basis for recognizing formal taxonomic taxa. Groups 2a, b, c are undoubtedly interrelated and their separation on anatomical grounds emphasizes the phylogenetic trends within the PEP-ck panicoid complex.

The following anatomical characteristics are diagnostic for this group:

(a) Four (rarely five or six) Kranz parenchyma bundle sheath cells surround each third order vascular bundle (Fig. 4a, b, d). The cells are arranged in a cross and are winged in the vertical and horizontal planes. The inner tangential wall is straight, whereas the other walls are inflated and elongated. The adaxial cell is often the largest.

(b) The first order bundles are surrounded by 8–10 parenchyma sheath cells, markedly smaller than those of the third order bundles (Fig. 4a, b, d).

(c) The specialized Kranz chloroplasts either entirely fill the outer sheath cells or are concentrated centrifugally around the outer tangential walls (Fig. 4a, b, d). Two different anatomical types have been recognized on ultrastructural grounds in *P. maximum* (Ariovich & Cresswell, 1981), probably reflecting this chloroplast difference. Individual chloroplasts are round, disc-like, and have a diameter at least 3× that of the mesophyll chloroplasts (Fig. 4a, b).

(d) Calcium oxalate crystals (Sanchez & Casabona, 1981) were not observed in the mesophyll or bundle sheath cells except in an older senescing leaf (Ellis, 1977).

(e) The third order vascular bundles are distinctly square in shape (Fig. 4a, b, c).

(f) A keel is always present, this semicircular and incorporating three large bundles (Wilson, 1976).

(g) Microhairs are exceptionally long (75–120 μm), thin, and elongated with the distal cell thin-walled, tapering, and equal in length to the basal cell (Fig. 4d). This agrees with the description given by Jauhar & Joshi (1968).

(h) Silica bodies are usually dumbbell-shaped but most specimens have few to many elongated nodular silica bodies as in Figure 4h.

(i) Intercostal hooks (Fig. 4c), costal prickles, and macrohairs also occur frequently. The macrohairs are of two types, being either cushion based or only associated with two modified epidermal cells. The latter type is also swollen basally.

Included species:

Panicum infestum Peters (Fig. 4d). A densely tufted perennial usually with conspicuous tubercle-based hairs. It has the upper lemma transversely rugose (Clayton & Renvoize, 1982) and therefore conforms both anatomically and morphologically to the group Brown (1977) considers as belonging to *Brachiaria.*

ZIMBABWE. 2130: Nuanetsi (DA), *Ellis 1308.*

Panicum maximum Jacq. (Fig. 4a–c). Very variable in vegetative characters such as size, hairiness, and growth habit. The structure of the spikelet is uniform, with the conspicuously transversely rugose upper lemma distinguishing *P. maximum* from all other species of *Panicum* in South Africa. Widely distributed in southern Africa, where it is found in a variety of habitats. Typically *P. maximum* grows in shady places, most frequently in open woodland.

TRANSVAAL. 2229: Waterpoort (DC), *Ellis 3477*; Zoutpansberg (DD), *Ellis 3850.*—2330: Levubu (AB), *Ellis 3853*; Tzaneen (CA), *Ellis 1592.*—2428: Warmbaths (CD), *Ellis 3920.*—2528: Pretoria, Wonderboom (CA), *Ellis 125*; Brummeria, *Ellis 762*; Roodeplaat (CB), *Ellis 1782.* NATAL. 3030: Warner Beach (CB), *Ellis 67*; Port Shepstone (CD), *Ellis 1466.*

Discussion. Panicum maximum and *P. infestum* are the only two South African species of *Panicum* examined in this study with the upper lemma transversely rugose. The species of Group 2b (*P. deustum*) and Group 2c (*P. dregeanum* and *P. fluviicola*) have pale, glossy upper lemmas. Therefore, those species with only four parenchyma sheath cells around the third order bundles are also the only *Panicum* species with transverse ridges or wrinkles on the upper lemma (Table 2). This anatomical structure for *P. maximum* has been illustrated by Morgan & Brown (1979), Ralph (1983), and Wilson et al. (1983).

Brachiaria chusqueoides (Hack.) W. D. Clayton, recently transferred from *Panicum* (Clayton, 1980), also has rugose upper lemmas and an identical bundle sheath configuration to that described for this particular group. From leaf anatomy it appears as if *P. obumbratum* Stapf deserves the same taxonomic treatment as *B. chusqueoides,* which it also resembles morpho-

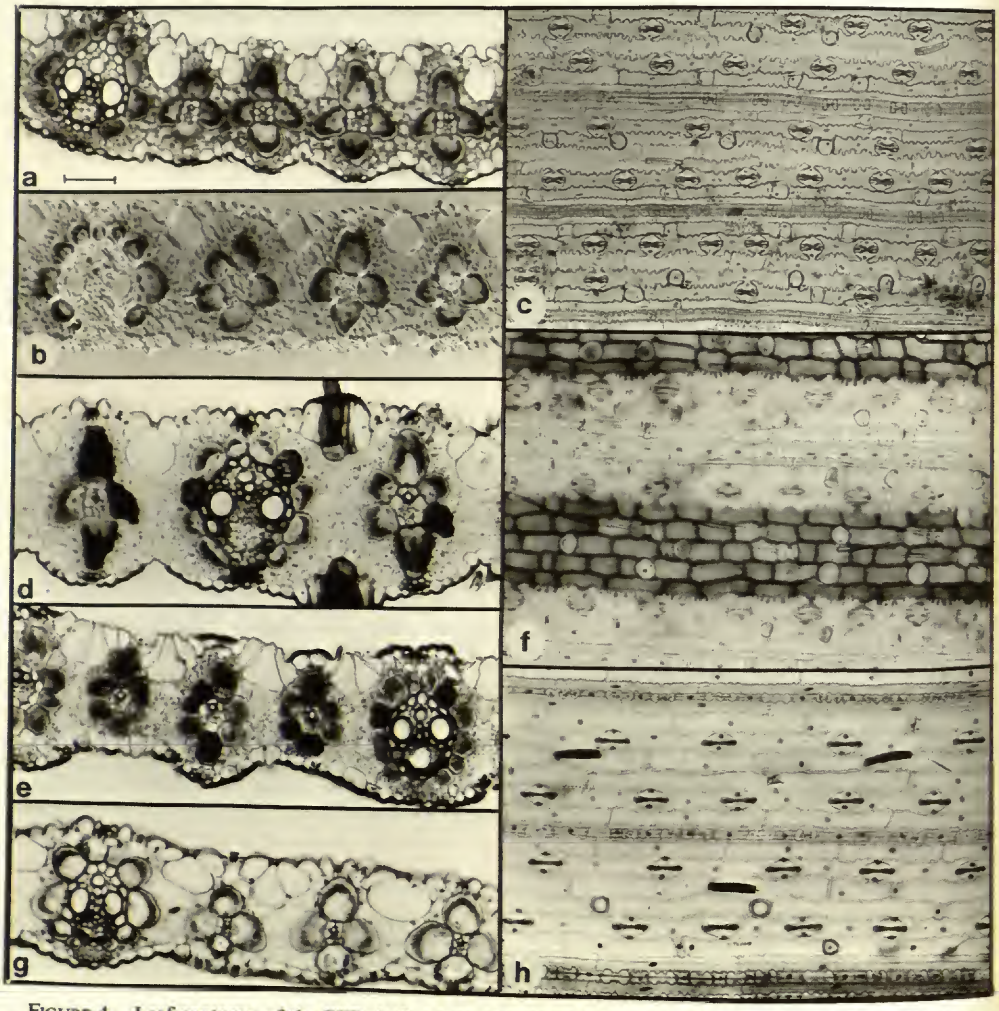

FIGURE 4. Leaf anatomy of the PEP-ck C_4 panicoid species belonging to Groups 2a and 2b.—a–d. Group 2a.—a–c. *P. maximum.*—a, b. Transverse sections; a, *Ellis 3920* with only four Kranz cells associated with the third order vascular bundles; b, *Ellis 1592* with four or five outer bundle sheath cells around the minor bundles; c, *Ellis 3920*, epidermal scrape showing elongated basal cells of microhairs, intercostal hooks and silica bodies.—d. *P. infestum, Ellis 1308*, with leaf anatomy similar to *P. maximum.*—e, f. Group 2b, *P. deustum, Ellis 3480*; e, note number of outer sheath cells surrounding third order bundles; f, epidermis with very thin, elongated microhairs.—g, h. *Brachiaria grossa, Ellis 1310* for comparative purposes. Scale = 50 μm.

logically (Chippindall, 1955). *Brachiaria grossa* Stapf (Fig. 4g, h) is another species of *Brachiaria* with coarsely rugose upper lemmas and an outer bundle sheath consisting of only four cells around the third order vascular bundles. It also resembles *P. maximum* in epidermal structure (Fig. 4h). *Panicum maximum* therefore resembles species of *Brachiaria* more closely than it does other PEP-ck *Panicum* species (Table 2).

These are the only grasses known to possess this type of anatomy. However, if the definition is broadened to include six (rarely seven) parenchyma sheath cells, then a number of additional *Brachiaria* species, all with rugose, rugulose, or granulose lemmas, can also be included with these species of Group 2a (Table 2). Widening the anatomical definition should be acceptable, as six outer sheath cells are sometimes found in species which normally have only four, such as *P. infestum* (Fig. 4d). It is of significance to note that

those species with the most rugose lemmas have only four sheath cells and there is a definite gradation in both these characters as we move away from species that conform strictly to this group.

Additional *Brachiaria* species that can be incorporated into this group are *B. arrecta* (Dur. & Schinz) Stent, *B. brizantha* (A. Rich.) Stapf (Ellis, 1977), *B.* (*Pseudobrachiaria*) *deflexa* (Schumach.) Robyns, *B. marlothii* (Hack.) Stent, *B. nigropedata* (Fical. & Hiern.) Stapf (Ellis, 1977), *B. xantholeuca* (Schinz) Stapf, and many others from tropical Africa. In none of these is the roughness of the upper lemma as pronounced as in the previous category.

The leaf anatomy of the genus *Urochloa* also conforms very closely to this group. This applies to all the southern African species, all of which have rugulose lemmas (Clayton & Renvoize, 1982) and are PEP-ck species. This genus undoubtedly belongs to this grouping.

Eriochloa is another genus that resembles this group in leaf anatomy. All species are PEP-ck and have only six outer sheath cells surrounding the third order vascular bundles. They also have elongated microhairs, nodular silica bodies, and the macrohairs with swollen bases are only associated with two specialized epidermal cells. Crystals are commonly found in the mesophyll cells. These characteristics all indicate relationships with this group, and Gutiérrez et al. (1976) have suggested that *Eriochloa* belongs with *Brachiaria* and the section *Fasciculata* of *Panicum*. However, *Eriochloa* has crustaceous, papillose upper lemmas (Clayton & Renvoize, 1982). Chippindall (1955) considered these lemmas to be finely pitted and ridged. It may just be possible to accommodate this genus in the definition of this group.

Several anatomical features vary in association with an increase in the number of bundle sheath cells surrounding the smaller bundles. These bundles become angular instead of square and the keels are reduced in many species. Of interest is the presence of crystals in the mesophyll and Kranz sheath cells of many of the taxa included here. This variation brings this group close to Group 2b, whereas a comparison of only *Panicum* species does not indicate this link. It appears as if *P. maximum* and *P. infestum* are closer to many *Brachiaria* species than they are to *P. deustum* of Group 2b.

This study therefore supports the suggested combination of all the PEP-ck panicoid species with rugose lemmas into a single genus, possibly *Brachiaria* (Gutiérrez et al., 1976; Brown, 1977). There are exceptions, however, and some species without rugose fertile lemmas from Group 2b appear to warrant inclusion and not all PEP-ck Paniceae belong in this category.

GROUP 2b

This group includes only *Panicum deustum* Thunb., a species with a pale, smooth, glossy upper lemma, and which consequently is not considered to belong with the taxa of Group 2a. Brown (1977) considers *P. deustum* of doubtful taxonomic position. It has been included in section *Clavelligerae*, which is characterized by having clavate glandular hairs. The species of this section appear to be non-Kranz (Brown, 1977), possess multicellular glandular hairs (Kabuye & Wood, 1969), and are classified in Group 1c of this study. *Panicum deustum*, however, is Kranz of the PEP-ck type and has only unicellular hairs. It clearly does not belong in section *Clavelligerae*.

Anatomical characteristics. Panicum deustum has the following anatomical characteristics, which serve to distinguish it from the species of Group 2a:

(a) Six or seven parenchyma sheath cells surround the third order vascular bundles (Fig. 4e). These cells are inflated, irregular, with the dorsal and sometimes the basal cell somewhat winged.

(b) The outer bundle sheath cells of the first order vascular bundles are not smaller in size than those of the third order bundles (Fig. 4e).

(c) The Kranz chloroplasts usually fill the outer bundle sheath cells (Fig. 4e) but are sometimes centrifugally located. These cells are often entirely filled with a dense, amorphous, black substance (Fig. 4e).

(d) Crystals are not present in any of the mesophyll or bundle sheath cells.

(e) The third order bundles are angular in shape (Fig. 4e) and not square as in the previous group.

(f) A keel similar to that described for *P. maximum* is always present.

(g) Microhairs are exceptionally long, with the basal cell alone longer than 50 μm, and total hair length can reach 150 μm (Fig. 4f).

(h) The silica bodies are dumbbell-shaped or nodular.

(i) Intercostal hooks (Fig. 4f) and macrohairs with swollen bases associated with a few specialized epidermal cells are present. Cushion-based macrohairs were not seen on any of the specimens examined anatomically.

Included species:

Panicum deustum Thunb. (Fig. 4e, f). This is the only species included in this group. No other *Panicum* species from southern Africa appears to be closely related to *P. deustum* on either anatomical or morphological grounds.

TRANSVAAL. 2329: Louis Trichardt (AB), *Ellis 3480.*—2330: Tzaneen (DC), *Ellis 1590.*—2531: Barberton (CB), *Ellis 1547*; Ida Doyer Nat. Res. (CC), *Ellis 389.* NATAL. 2732: Tongaland, Black Rock (BB), *Ellis 4061*; Sordwana Bay (DA), *Ellis 1129.*—2831: Mtunzini (DD), *Ellis 3385.* CAPE. 3227: Komga (DB), *Ellis 1104.*

Discussion. Panicum deustum differs from Group 2a basically only in the outer bundle sheath cell number and configuration. Visually this is striking but intermediates do occur and the two character states intergrade completely. This is therefore an artificial subdivision but it helps to emphasize that the species of Group 2a are very closely linked to certain *Brachiaria* species, which in turn show relationships with other *Brachiaria* species, *Urochloa* and *Eriochloa* (Table 2). Some further *Brachiaria* species are intermediate between these latter species and *P. deustum.* Examples are *B. advena* Vickery, *B. eruciformis* (J. E. Sm.) Griseb., *B. malacodes* (Mez. & K. Schum.) Scholz, *B. schoenfelderi* C. E. Hubb. & Schweick., and *B. serrata* (Thunb.) Stapf. All these species have smooth, shiny upper lemmas as has *P. deustum.* All these *Brachiaria* species differ little anatomically and this observation implies that the suggestion that all PEP-ck panicoid species with transversely rugose fertile lemmas should be transferred to *Brachiaria* (Brown, 1977) is not strictly true, as some species with smooth glossy lemmas also appear to belong to this assemblage. The only discernible difference between these *Brachiaria* species is that the outer bundle sheath cells of the Group 2b species are more numerous (usually eight), rounder, and the outer bundle sheath is a distinct Kranz or ring of cells of uniform size and shape. Chloroplasts are dense and crystals are often developed. These are not absolute differences and all degrees of intermediates occur.

Tricholaena is another panicoid genus that appears to belong in this group. It has very similar leaf anatomy to that described for *P. deustum* and conforms most closely to this group in leaf anatomy. *Panicum deustum* is clearly more closely related to species of *Brachiaria* than it is to any other southern African *Panicum* species. Its phylogenetic relationships are not readily inferred from leaf anatomy or spikelet morphology but it certainly does not belong to any of the C_3 species of Group 1. Its relationships must lie with this complex of PEP-ck panicoid grasses, which constitute a closely knit assemblage of interrelated taxa.

GROUP 2c

This group includes only two southern African species of *Panicum, P. dregeanum* and *P. fluvicola.* These are densely tufted perennials of damp, swampy tropical grasslands. Their upper lemma is pale and glossy and not rugose as in Group 2a. In this respect this group resembles *P. deustum* of Group 2b.

Anatomical characteristics. This group can be separated from the other groups of PEP-ck *Panicum* species by the following anatomical criteria:

(a) The third order vascular bundles are surrounded by 7–9 outer bundle sheath cells. Either first, second, and third order bundles may occur (Fig. 5a), or only first and third order bundles. These second order bundles are surrounded by 12 parenchyma sheath cells and the third order bundles by seven cells.

(b) Outer sheath cells of all orders of bundle are similar in size and shape (Fig. 5a).

(c) Kranz chloroplasts are peripherally located in a distinctly centrifugal manner (Fig. 5a).

(d) Arrangement of the vascular bundles is distinctive, with three bundles (rarely five) separating successive first order bundles. There may be two third order bundles and one second order bundle (Fig. 5a) or 3–5 third order bundles. In the previous two groups, 6–9 small bundles are located between the first order bundles.

(e) Third order bundles are angular in shape (Fig. 5a) and not square as in *P. maximum.*

(f) Crystals are sometimes present in the outer sheath cells.

(g) In *P. dregeanum* well-developed adaxial ribs and furrows are present, with the furrows overlying the third order bundles (Fig. 5a). In *P. fluviicola* all bundles are of similar size and the ribs are not so accentuated.

(h) Microhairs are usually absent (Fig. 5b) and, if present, the basal cell is very short (about 10 μm).

(i) Silica bodies are tall and narrow (Fig. 5b) but are sometimes cross-shaped or shortly dumbbell-shaped.

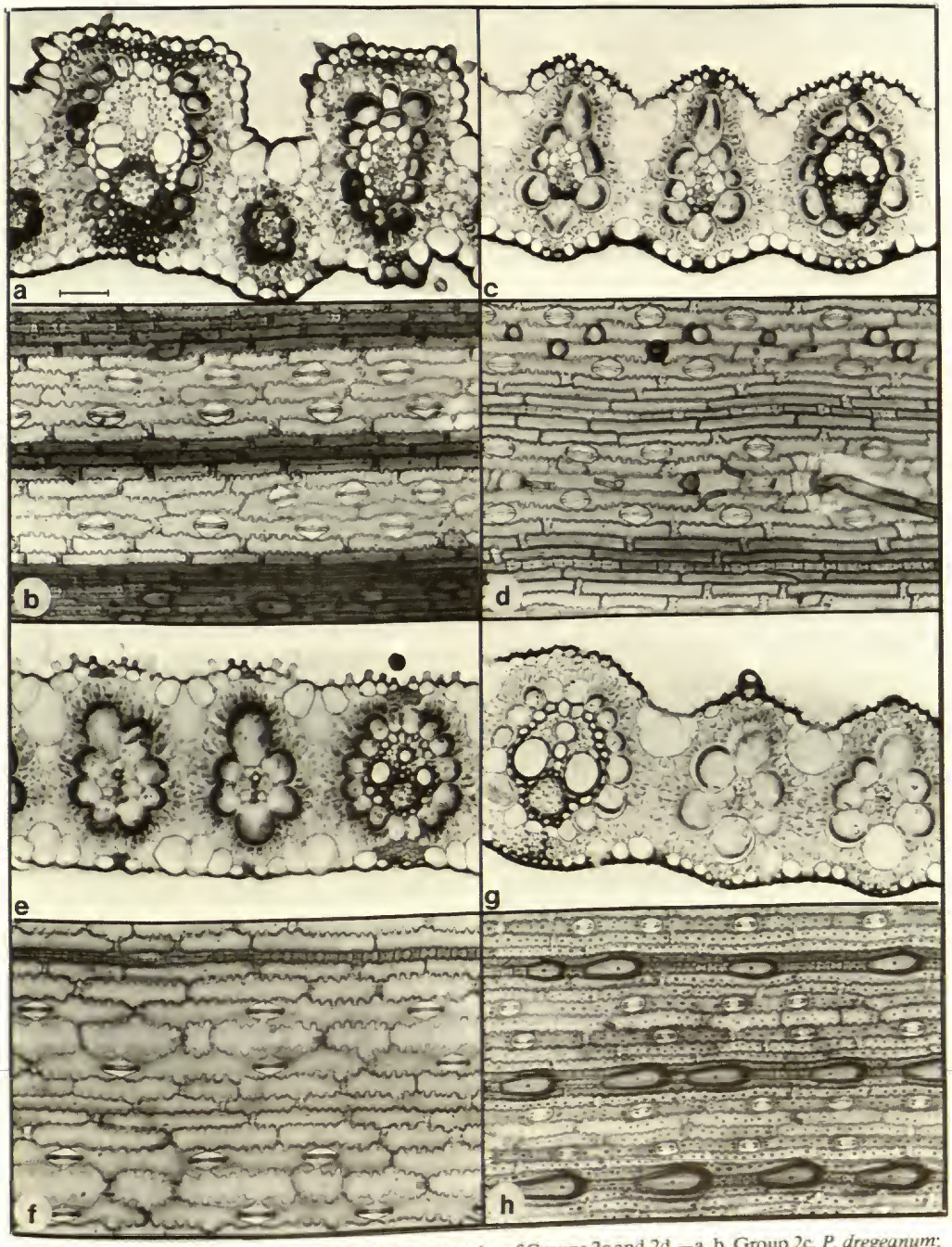

FIGURE 5. Leaf anatomy of PEP-ck C_4 *Panicum* species of Groups 2c and 2d.—a, b. Group 2c, *P. dregeanum*; a, *Ellis 3502* with adaxial ribs and furrows and first, second and third order vascular bundles; b, *Ellis 4421*, with very short basal cells of microhairs, without abaxial papillae and crystals in the outer sheath cells; f, *Ellis 1842*, with very sinuous long cell walls.—g, h. *P. subalbidum*; g, *Ellis 1467*, note centrifugal specialized chloroplasts; h, *Ellis 1925* with abaxial papillae and costal prickles. Scale = 50 μm.
epidermis with tall and narrow silica bodies and with microhairs.—c–h. Group 2d with markedly centrifugal chloroplasts and adaxial papillae.—c, d. *P. repens*; c, *Ellis 3503*; d, *Ellis 3711* with microhairs and base of macrohair.—e, f. *P. schinzii*; e, *Ellis & Loxton 940* with accentuated peripheral chloroplast position and with

(j) Epidermal appendages are rare, but hooks and prickles and macrohairs are sometimes developed. Macrohairs are of the normal cushion-based type associated with many modified epidermal cells.

Included species:

Panicum dregeanum Nees (Fig. 5a, b). Distinctive anatomy with adaxial ribs and furrows and large size difference between first and third order bundles. This species appears to be confined to moist habitats.

TRANSVAAL. 2428: Nylstroom (BD), *Ellis 3502.*—2529: Loskop Dam (AD), *Ellis 2079.*—2730: Piet Retief (BB), *Ellis 4079.* NATAL. 2831: Empangeni (DC), *Ellis 3389, 3390.*—2930: Pietermaritzburg (CB), *Ellis 4421.*—3030: Umdoni Park (CC), *Ellis 3799.*

Panicum genuflexum Stapf. This species differs from *P. dregeanum* in having branched culms. It is only known from Lake St. Lucia, where it occurs in hygrophilous grassland in seeps in black, humic soils. It resembles *P. fluviicola* closely in leaf anatomy.

NATAL. 2832: Lake St. Lucia (AD), *Ellis 3413, 4498.*

Panicum fluviicola Steud. A species of seasonally inundated grasslands often on sandy, alluvial soils. Leaf anatomy without the second order vascular bundles or adaxial ribs as in *P. dregeanum.* The specimen from Natal resembles *P. dregeanum* most closely.

S.W.A. 1723: Caprivi Zipfel (CD), *Ellis 312.*—1724: Caprivi Zipfel (CC), *Ellis 3729.*—1824: Caprivi Zipfel (AA), *Ellis 3694.* NATAL. 2732: Tongaland (BA), *Ellis 4058.*

Discussion. Anatomically this group differs substantially from Groups 2a and 2b, particularly in vascular bundle arrangement and epidermal structure. The very short microhairs are also significant and do not suggest a close relationship between these three groups. Therefore, a comparison of the anatomy of the PEP-ck *Panicum* species only does not suggest affinities between *P. dregeanum* and *P. fluviicola* and those *Panicum* species with rugose lemmas. However, if the anatomy of other PEP-ck panicoid grasses is taken into consideration as well, then a group of intermediate species of *Brachiaria* is evident, which links this group to the rugose lemma, PEP-ck panicoid grasses (Table 2). Examples are *B. dictyoneura* (Fig. & De Not.) Stapf, *B. dura* Stapf, *B. humidicola* (Rendle) Schweick., and *B. subulifolia* (Mez.) Clayton. These species also have only 3–5 bundles separating successive first order bundles and most of them also have second order bundles. Adaxial ribs and furrows are common and there is a tendency towards permanently infolded leaves, as in *B. dura,* with thick abaxial cuticles.

The allies of *Panicum dregeanum* and *P. fluviicola* should be sought among this group and not with the other PEP-ck *Panicum* species. Once again, PEP-ck *Panicum* species appear to show closer affinities to groups within *Brachiaria* than they do with other *Panicum* species. There are some other *Panicum* species that appear to belong with *P. dregeanum* and *P. fluviicola,* and this combined group may constitute the "Diffusa" group of Brown (1977). An African example may be *P. griffonii* Franch. (Clayton & Renvoize, 1982).

From the anatomical evidence it seems possible that the inflorescence characters used in separating *Panicum* and *Brachiaria* are artificial and require re-evaluation. *Panicum dregeanum* and *P. fluviicola* both have pale, glossy lemmas. It is notable that the *Brachiaria* species that show anatomical similarities with these *Panicum* species also have smooth, shiny or glossy lemmas as in *B. subulifolia. Brachiaria humidicola* and *B. dictyoneura* have slightly papillose upper lemmas (Clayton & Renvoize, 1982).

The *Brachiaria* species with Group 2b and 2c anatomy are not consistent for this lemma character, and species with smooth, glossy lemmas occur in both groups. This is the main reason why the separation of Groups 2b and 2c has not been made more definite (Table 2). These anatomical groupings may perhaps only reflect very recent evolutionary trends that are not yet taxonomically distinct. It may not be feasible to assign taxonomic status to these groups, but they should nevertheless be taken into account in any taxonomic treatment.

GROUP 2d

This is a very distinct group which appears to have no close affinities with the other groups of *Panicum* with PEP-ck type anatomy (Table 2). The species included in this complex form a coherent taxonomic entity with similar anatomy, morphology, and ecology. All are hydrophytic, preferring damp or even aquatic habitats, and all have pale and glossy upper lemmas. This group shows little anatomical resemblance to any of the other *Panicum* groups or even other panicoid

genera. The component species appear to constitute a separate genus not allied to the group of interrelated species that is linked to those panicoid taxa with rugose lemmas, even though all these species have classical PEP-ck type anatomy.

Anatomical characteristics. All species included in this group display very similar anatomy. This is characterized by very rounded, inflated outer bundle sheath cells with exaggerated centrifugal chloroplasts. The epidermis differs greatly from the previous PEP-ck groups, and papillae, particularly adaxial papillae, are present on all taxa. An anatomical circumscription of this group is as follows:

(a) Six regular, round, inflated Kranz cells surround the third order vascular bundles in all species (Fig. 5e, g) except *P. repens,* which has 7–11 irregular outer sheath cells around the smaller bundles (Fig. 5c).

(b) The first order vascular bundles are surrounded by 15–17 outer sheath cells (Fig. 5e, g) except in *P. repens,* where only 10–12 cells surround the larger bundles.

(c) The Kranz chloroplasts characteristically lie very close to the outer tangential cell wall, often forming only a thin peripheral layer and occupying only a small proportion of the cell area (Fig. 5e, g). In *P. repens* these chloroplasts are proportionally much larger (Fig. 5c).

(d) Calcium oxalate crystals are sometimes present in the outer sheath cells of older, senescing leaves.

(e) A distinctive, well-developed keel is always present in *P. subalbidum,* seldom in *P. schinzii,* and never in *P. repens.*

(f) Papillae on the adaxial epidermal cells are developed in all species (Fig. 5c, e, g).

(g) The epidermal structure is variable (Fig. 5d, f, h) but consistent and diagnostic for each of the species included in this group. An example is microhair length in which the basal cells are 10–25 μm in *P. repens* (Fig. 5d), less than 10 μm in *P. schinzii* (Fig. 5f) and *P. subalbidum* (Fig. 5h), but up to 50 μm in *P. gilvum.*

Included species:

Panicum gilvum Launert. Resembles *P. schinzii* closely in leaf anatomy but is unusual in possessing very long microhairs as well as macrohairs. A true hydrophyte, floating on the surface of open water in pans.

BOTSWANA. 1823: Chobe Natl. Park (DB), *Ellis 2916.* S.W.A. 2117: Okahandja (DD), *Gibbs Russell & Smook 5354.*

Panicum impeditum Launert. Anatomy identical to that of *P. schinzii* in both transverse section and epidermis structure. The exact identity of this species appears to be somewhat uncertain and it is possible that some of the specimens identified as *P. schinzii* should be included here.

CAPE. 2722: Olifantshoek (DC), *Botha & Panagos 50.*

Panicum repens L. (Fig. 5c, d). This species differs somewhat from the other species of this group in both transection and epidermal structure. Its inclusion in this group is tentative but it does have the adaxial papillae of this group and it undoubtedly belongs near the other species included in this group.

S.W.A. 1724: Caprivi Zipfel (CB), *Ellis 3711.*—1824: Caprivi Zipfel (AA), *Ellis 3696.* TRANSVAAL. 2328: Villa Nora (CA), *Smook 4211.*—2428: Nylstroom (BD), *Ellis 3503, 3504;* Warmbaths (CD), *Ellis 3919.*—2625: Barberspan (DA), *Ellis 3629.* NATAL. 2831: Mtunzini (DD), *Ellis 3379.*—2832: Lake St. Lucia (BA), *Ellis 3400, 3401, 4488.*

Panicum schinzii Hack. (Fig. 5e, f). This species forms the core of this complex, and although it is taxonomically very variable, its anatomy is consistent throughout the sample studied. Eight of the voucher specimens did not key out satisfactorily and were not identified as *P. schinzii* but were included in this species on the basis of anatomy. Indications are that *P. schinzii* requires taxonomic revision. It is the least hydrophytic of all the members of this group and has become a weed of agriculture, particularly in irrigated lands.

TRANSVAAL. 2231: Kruger Natl. Park, Pafuri (CB), *Ellis 3218, 3856, 3857.*—2327: Ellisras (BC), *Smook 4271.*—2428: Warmbaths (CD), *Ellis 3912, 3918.*—2431: Kruger Natl. Park, Nwanedzi (BD), *Ellis 3549.*—2528: Rust der Winter (BA), *Ellis 3900, 3901;* Onderstepoort (CA), *Ellis 1821.*—2530: Belfast (CA), *Ellis 4105.*—2729: Standerton (BA), *Ellis 1507;* Majuba Pass (BD), *Ellis 205.* O.F.S. 2728: Villiers (AB), *Smook 4799.*—2827: Ficksburg (DD), *Ellis & Loxton 940.* CAPE. 2722: Olifantshoek (DC), *Botha & Panagos 43.*—3029: Kokstad (AD), *Ellis 230.*

Panicum sp. aff. *P. schinzii.* These specimens have *P. schinzii* anatomy but differ in morphology. They certainly belong to this complex and cannot be distinguished anatomically from typ-

ical *P. schinzii*. The collection *Gibbs Russell & Smook 5108* may prove to be extremely interesting, as it has a very conspicuous Kranz sheath with the chloroplasts almost filling these cells. It closely resembles the NAD-me type but has an epidermis identical to that of *P. schinzii*.

S.W.A. 2819: Warmbad (BA), *Gibbs Russell & Smook 5108*. TRANSVAAL. 2530: Belfast (CA), *Ellis 4103, 4104*.

Panicum subalbidum Kunth (Fig. 5g, h). A species closely related to *P. schinzii* but differing in the possession of abaxial as well as adaxial papillae and other epidermal features. Leaf anatomy is very close to this complex and it certainly belongs here.

TRANSVAAL. 2230: Kruger Natl. Park, Punda Milia (DB), *Ellis 1925*.—2231: Kruger Natl. Park, Pafuri (AC), *Ellis 563*.—2328: Villa Nora (CA), *Smook 4209*.—2428: Warmbaths (CD), *Ellis 3913*.—2430: Mt. Sheba (DC), *Ellis 4463*.—2528: Roodeplaat (CB), *Ellis 3893*.—2529: Loskop Dam (AD), *Ellis 3870*. NATAL. 2832: Lake St. Lucia (AD), *Ellis 4504*.—3030: Port Shepstone (CD), *Ellis 1467*. TRANSKEI. 3128: Umtata (DB), *Ellis 259*.

Panicum sp. aff. *P. subalbidum*. Specimens lacking abaxial papillae but probably very close to *P. subalbidum*.

S.W.A. 1724: Caprivi Zipfel (DC), *Ellis 3732*. NATAL. 2832: Lake St. Lucia (AD), *Ellis 4506*.

Discussion. *Panicum repens* stands out from the rest of the species classified in this group in both cross-sectional anatomy and epidermal structure. The possession of adaxial papillae, however, indicates affinities with this group and it undoubtedly belongs closer to this than to any of the other PEP-ck *Panicum* groups.

Panicum repens belongs to section *Repentia* of subgenus *Panicum* (Brown, 1977). Other species of this anatomical assemblage (Group 2d) belong to the "*Dichotomiflora*" group of the same subgenus. They are closely related and this is confirmed by the leaf anatomy. The treatment of *P. repens* in a separate section is supported by its unusual leaf anatomy. No other southern African species appear to belong to section *Repentia*, but *P. subflabellatum* Stapf, *P. pinifolium* Chiov., and *P. repentellum* Napper from tropical Africa may belong with *P. repens* in this section (Clayton & Renvoize, 1982). These all have stiff leaf blades and occur in coastal or in either fresh or brackish inland aquatic habitats.

Panicum schinzii, *P. subalbidum*, and the other species of Group 2d are clearly very closely related but do not show anatomical similarities with any other panicoid grasses. They appear to form a rather isolated group with no obvious relatives in the genus *Panicum*.

The distinct anatomy of Group 2d and the absence of obvious phylogenetic links is ignored by their classification in the "*Dichotomiflora*" group together with *P. coloratum* and its allies, which have centripetal chloroplasts and NAD-me photosynthesis (Ohsugi et al., 1982). NAD-me species are placed in Group 3a here, and close affinities between these two groups of species are unlikely in light of my observations on the rest of the genus. However, caution is called for, as certain reports in the literature suggest that species of Group 2d are actually NAD-me species (Ohsugi et al., 1982) although they have centrifugal chloroplasts, which are supposedly perfectly correlated with the PEP-ck C_4 photosynthetic type (Ellis, 1977; Hattersley & Browning, 1981).

Brown (1977) included *Panicum schinzii*, *P. subalbidum*, and others with centrifugal chloroplasts in subgenus *Panicum*, which has NAD-me type photosynthesis. He did not comment on their chloroplast arrangement or biochemical typing but considered this group to be very homogeneous, all taxa being P.S. (with a double bundle sheath) and with smooth and shiny fertile lemmas. Ohsugi et al. (1982) investigated the decarboxylating enzymes of *P. schinzii* (= *P. laevifolium*) and *P. subalbidum* (= *P. longijubatum*) and classified both biochemically as NAD-me species, despite their centrifugal chloroplasts. Four accessions of *P. coloratum* examined by these authors had centrifugal chloroplasts, whereas none in my sample of 20 specimens had this chloroplast arrangement. The illustration of *P. coloratum* published by Ohsugi et al. (1982) is identical with that of Group 2d, but the illustrations of Barnard (1964) and Hattersley (1984) show *P. coloratum* with centripetal chloroplasts. Hattersley & Browning (1981) and Hattersley (1984) classify *P. schinzii* (= *P. laevifolium*) as a PEP-ck species and consider all the other *Dichotomiflora* group to be NAD-me species (*P. coloratum*, *P. dichotomiflorum*, *P. kalaharense*, *P. lanipes*, and *P. stapfianum*). This completely agrees with my findings. The biochemical typification of *P. schinzii* and *P. subalbidum* urgently requires verification.

Panicum schinzii has all the anatomical and ultrastructural features associated with the PEP-ck subtype (Hattersley & Browning, 1981). The Kranz chloroplasts are predominantly centrifu-

gal or evenly distributed. Bundle sheaths double with granal thylakoids in stacks in Kranz cell chloroplasts. Mitochondrial frequency is high with the mitochondria associated with the chloroplasts. *Panicum schinzii* also has a suberin lamella present in the Kranz cell walls. It therefore appears reasonable to consider *P. schinzii* to belong to the PEP-ck type until proven otherwise.

If the species of Group 2d do prove to be NAD-me species, then they will be the first known exceptions to the correlation between this type of anatomical structure and PEP-ck type photosynthesis. A specimen of *Panicum* sp. aff. *P. schinzii* (*Gibbs Russell & Smook 5108*) of uncertain identity may be extremely significant in this regard. It appears to be intermediate between the exaggerated PEP-ck type anatomy of Group 2d and the NAD-me type of the *P. coloratum* group. The Kranz chloroplasts virtually fill the outer sheath cells, although they are definitely more concentrated centrifugally. The epidermis is undoubtedly of the *P. schinzii* type. The collection locality of this plant is from the dry, semi-desert Upington district where NAD-me *Panicum* species are common, although it was growing in a damp, muddy depression, which is a typical habitat for *P. schinzii*.

Further studies are needed on the biochemistry and taxonomy of this group. It is nevertheless clear that these species do not belong with the PEP-ck *Panicum* species associated with the rugose lemma panicoids (Groups 2a, 2b, 2c). The species of Group 2d do not appear to show affinities with any other panicoid grasses except perhaps *P. coloratum* and the *Dichotomiflora* group. Although differing considerably in anatomy with centrifugal and centripetal chloroplasts, there are indications that these two groups have morphological and photosynthetic similarities, and this possibility urgently requires confirmation.

Group 3

All the *Panicum* species with double bundle sheaths, centripetally located Kranz chloroplasts, and the NAD-me subtype of the C_4 photosynthetic pathway are accommodated in this group. The southern African *Panicum* species belonging to this group appear to be very closely allied and have very similar anatomy. They are most abundant in the drier western and central parts of the subcontinent and have a pale, glossy upper lemma. This group seems to be rather isolated within the Paniceae. *Oryzidium barnardii* C. E. Hubb. & Schweick. [incorrectly classified as a PEP-ck species, Ellis (1977)] and *Psilochloa pilgerana* (Schweick.) Launert are the only other southern African representatives of this tribe with NAD-me type anatomy. Other small panicoid genera such as *Chaetium* and *Scutachne* from the New World and *Thuarea* and *Spinifex* from Asia and Australia are also NAD-me (Brown, 1977). This anatomical and photosynthetic class is uncommon in the Paniceae.

This group, as here circumscribed, comprises the "true" *Panicum* species including *P. miliaceum* L., the type of the genus, also a NAD-me species. It is another group that does not have close affinities with other major groups of panicoid genera. Among the NAD-me panicoids it is undoubtedly the *Panicum* species of this group which constitute the core of the group. This is in marked contrast with Groups 1 and 2, where the *Panicum* species are strongly linked to associated species and even groups of genera.

Two anatomical groups have been identified within this group. The species linked to *Panicum coloratum* form a coherent and closely related complex and comprise the first group. Group 3b is a miscellaneous assemblage of those species not similar to *P. coloratum* and its allies. Some species of Group 3b may actually belong to the *P. coloratum* complex but have diverged sufficiently morphologically and anatomically from the *P. coloratum* type. These differences are not great and this tentative separation emphasizes the remarkable anatomical homogeneity of Group 3a as here circumscribed.

Group 3a

The constituent species cannot be separated easily on anatomical grounds in this unusually uniform group. This is not surprising, as the species are themselves very closely related and are often very difficult to separate morphologically. *Panicum coloratum* is the core of this category but it is highly variable and intergrades with most of the species related to it; the taxonomy of this complex is therefore rather confusing.

Anatomical characteristics. The anatomy of members of this group is virtually identical (Fig. 6). The various tissues correspond closely in size and arrangement, and the degree of variation between the four species illustrated is much less than is often encountered in a single species. The

anatomical diagnosis of the group is applicable to each of the constituent species. The following suite of characters distinguishes this from the other anatomical groups of *Panicum*:

(a) The Kranz sheath is a very conspicuous circular band or ring of large uniform cells (Fig. 6a, c, e, g). The individual sheath cells have straight radial walls, in contrast to the inflated walls of the PEP-ck species.

(b) The chloroplasts are densely packed, darkly staining, and concentrated against the inner tangential wall. Individual disclike chloroplasts cannot be distinguished (Fig. 6a, c, e, g).

(c) Three (rarely four or five) third order vascular bundles separate successive lateral first order bundles. There is a definite tendency for the central bundle of each of these groups of minor bundles to be slightly larger than the other two. In some instances this central bundle can be classified as a second order bundle (Fig. 6c, e).

(d) The vascular bundles are very close together, with the minimum distance less than 50 μm.

(e) Adaxial ribs are not pronounced (Fig. 6a, c, e, g).

(f) The adaxial epidermal cells are papillate and the abaxial cells are not.

(g) The minor bundles are not linked to the epidermis by sclerenchyma strands or girders (Fig. 6a, c, e, g) and this is reflected in the epidermal structure where long cell files overlying these costal areas are not differentiated in size or shape from the intercostal files except that they stain differently (Fig. 6b, d).

(h) The microhairs are rodlike with tapering distal cells. The total length of these hairs does not exceed 50 μm (Fig. 6b, d, f, h).

(i) Cushion-based macrohairs are common and occur on some specimens of most species.

Included species: All the *Panicum* species related to *P. coloratum* are included in this group. This includes species in which the lower glume is clasping and less than ⅓ the length of the spikelet. All these species also have pale and glossy upper lemmas and are anatomically very similar.

Panicum arcurameum Stapf. A very rare species only known from the Pretoria district. It has extremely hispid leaves with long, stiff tubercle-based hairs. There is a tendency for the number of smaller bundles between the larger bundles to be greater than three.

TRANSVAAL. 2528: Onderstepoort (CA), *Ellis 3881, 3883, 3904.*

Panicum coloratum L. var. *coloratum* (Fig. 6a, b). A highly variable, polymorphous species comprising several recognizable forms that intergrade into one another and with related species such as *P. lanipes* and *P. stapfianum.* It is remarkable that the total anatomical variation in all the specimens examined is so small in comparison with most other widespread, variable species. The anatomical variation of *P. coloratum* is nevertheless comparable to the total variation encountered in all the species of this group.

In the sample studied, the bulk of the specimens form a coherent, uniform anatomical entity. However, two additional and separate taxa appear to be included in this *P. coloratum* sample. Apart from being anatomically recognizable, both are morphologically distinct and occur in unusual habitats for *P. coloratum. Ellis 1914, 3216,* and *3855* differ from the rest of the *P. coloratum* sample in having wider leaves with 4–5 minor bundles between the larger bundles. The leaf margin tapers to a prominent point, which is not the case with other taxa of this group. The epidermal cells are narrower, more elongated, and less sinuous. All these specimens come from the Pafuri sandveld of the northern Kruger National Park, are found around pan margins and river banks, and have a distinctly grey foliage color. *Ellis 1783, 2905,* and *2912* resemble typical *P. coloratum* in transection but have prominent crenate-shaped intercostal silica bodies between the long cells. No other species of this group possesses this type of silica body or short cell. These grasses also appear to be hydrophytic, although *Ellis 1783* was not associated with water. The remainder and bulk of this large anatomical sample had anatomy similar to that illustrated in Figure 6a, b.

S.W.A. 1823: Caprivi Zipfel (BC), *Ellis 328.*—2519: Gibeon Dist. (AC), *Ellis 4364.* BOTSWANA. 1824: Chobe Natl. Park (CB), *Ellis 2912.*—1924: Moremi (AC), *Ellis 2905.* TRANSVAAL. 2230: Kruger Natl. Park, Levubu River (DB), *Ellis 1914.*—2331: Kruger Natl. Park, Machayi Pan (CB), *Ellis 3216, 3855.*—2428: Warmbaths (CD), *Ellis 3323*; Naboomspruit (DA), *Ellis 3327, 3332, 3924.*—2528: Roodeplaat Dam (CB), *Ellis 1783.*—2531: Kruger Natl. Park, Lower Sabie (BB), *Ellis 508.* O.F.S. 2728: Reitz (DA), *Smook 4633.*—2825: Dealsville (CA), *Ellis 3625.* NATAL. 2732: Mkuzi (CA), *Ellis 4522*; (CB), *Ellis 4542.* CAPE. 2624: Vryburg (DC), *Ellis 3584.*—2922: Prieska (DB), *Botha & Panagos 3.*—3325: Uitenhage (CD), *Smook 3807.*

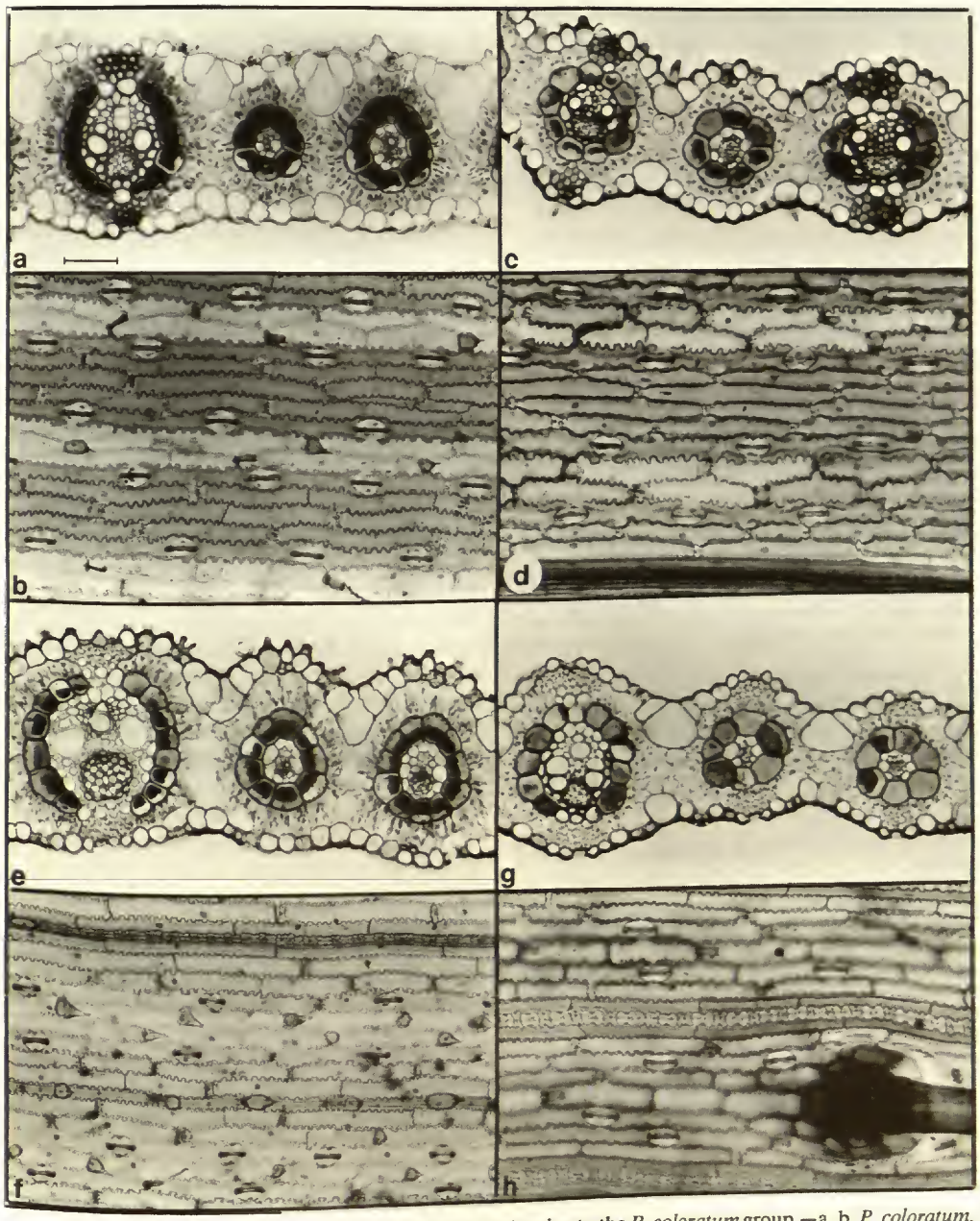

FIGURE 6. Group 3a, NAD-me C_4 *Panicum* species belonging to the *P. coloratum* group.—a, b. *P. coloratum, Ellis 3625*; a, centripetal chloroplasts and adaxial papillae; b, abaxial epidermis with intercostal zones and costal zones overlying second and third order bundles.—c, d. *P. stapfianum, Ellis & Loxton 976*; c, typical NAD-me structure; d, costal and intercostal zones similar to *P. coloratum*.—e, f. *P. lanipes*; e, *Ellis 4341* with centripetal chloroplasts and adaxial papillae; f, *Ellis 4340*, abaxial epidermis with costal and intercostal hooks.—g, h. *P. volutans, Ellis 2002*; g, NAD-me anatomy; h, macrohair base and microhairs visible. Scale = 50 μm.

Panicum lanipes Mez. (Fig. 6e, f). Inseparable from *P. coloratum* on leaf anatomical grounds and obviously closely allied to both *P. stapfianum* and some of the forms of *P. coloratum*. *Panicum lanipes* is characterized by having matted white wool at the bases of the leaf sheaths. Whether this character is consistent and reflects natural relationships is impossible to judge, but the leaf anatomy does not support the recognition of this species.

S.W.A. 2516: Helmeringhausen (DB), *Ellis 4340, 4341*. CAPE. 2820: Keimoes (BA), *Botha & Panagos 41*.—2921: Kenhardt (DA), *Botha & Panagos 15*.

Panicum stapfianum Fourc. (Fig. 6c, d). Also virtually identical to *P. coloratum* in leaf anatomy and morphology. Distinguished by its narrower leaf blades and very caespitose base. It is easily confused with some strains of *P. coloratum*, and leaf anatomy indicates that this separation may be rather artificial.

O.F.S. 2827: Clocolan Dist. (DC), *Ellis & Loxton 976*.—2926: Bloemfontein (AA), *van Heerden 90*. CAPE. 2823: Griekwastad (CC), *Ellis 3609*.

Panicum volutans J. G. Anders. (Fig. 6g, h). This species closely resembles *P. coloratum* anatomically but is very distinct morphologically. It is an annual with a very wide open panicle and stiff branches bearing spikelets only at the ends. This whole panicle breaks off when mature and is carried by the wind as a tumbleweed.

TRANSVAAL. 2428: Warmbaths (CD), *Ellis 2002, 3430*.—2528: Onderstepoort (CA), *Ellis 3882*.

Panicum spp. Most of the unidentified taxa included here are annuals from northern South West Africa/Namibia and may possibly belong to *P. novemnerve*. Anatomically all resemble *P. coloratum* very closely except that they do not have midribs. The specimens from the northern Cape obviously belong to the *P. coloratum* complex but do not key out to any of the described species.

S.W.A. 1817: Tsumeb (CD), *Smook 5153*.—1915: Etosha Pan (BB), *Smook 5109*.—1916: Etosha Pan (A), *Smook 5110, 5120*.—1917: Otavi (CA), *Smook 5163*.—2015: Outjo Dist. (AB), *Gibbs Russell & Smook 5268*; (DD), *Smook 5108*.—2116: Omaruru Dist. (AA), *Gibbs Russell & Smook 5235*. CAPE. 2520: Kalahari Gemsbok Natl. Park (DA), *Ellis 4366*.—2823: Griekwastad (CC), *Ellis 4326*.

Discussion. The anatomy of *Panicum coloratum* as described here for southern African specimens is identical to that of a specimen grown at the Royal Botanic Gardens, Kew (Garden No. 321-72.04366), as well as illustrations of the species published by Barnard (1964) and Hattersley (1984). Ohsugi et al. (1982) illustrate *P. coloratum* var. *makarikariense*, which also matches this anatomy very closely. The *P. coloratum* complex, therefore, is remarkably consistent in leaf anatomy and forms a homogeneous anatomical and morphological entity, possibly deserving separate subgeneric rank apart from *P. miliaceum* and the remainder of the subgenus *Panicum*. The species of Group 3a are definitely distinct and not phylogenetically close to the *Panicum* species of Groups 1, 2, and 4.

Panicum coloratum and its allies belong to the *Dichotomiflora* group of subgenus *Panicum*. Some species with PEP-ck type anatomy are presently also included in this group. As discussed under Group 2d, these species should be removed to a separate and anatomically discrete group, probably of generic rank. The remaining species of the *Dichotomiflora* group should be recognized as a section distinct from section *Panicum*, which in southern Africa includes *P. miliaceum*, the type of *Panicum*. The separation of *P. coloratum* and *P. miliaceum* in different sections is supported by the anatomical evidence. The two groups differ sufficiently at the anatomical level to be regarded as distinct subgenera.

The annual species, *Panicum arcurameum* and *P. volutans*, are included in the *P. coloratum* group in this study but were included in section *Panicum* by Brown (1977). They agree closely in leaf anatomy with the *P. coloratum* group and it appears as if virtually all the African NAD-me *Panicum* species belong to this section. *Panicum novemnerve* was placed in section *Panicum* by Brown (1977), and if any of my unidentified specimens from South West Africa/Namibia are in fact this species, then *P. novemnerve* should also be transferred to the *Dichotomiflora* group. *Panicum virgatum*, section *Panicum*, was also examined and it closely resembles *P. coloratum* and its allies.

Panicum miliaceum (Fig. 7c), although a NAD-me species, is not part of this complex of species centered around *P. coloratum*. It is here treated separately in Group 3b.

GROUP 3b

All southern African NAD-me *Panicum* species that do not closely resemble *P. coloratum* in leaf

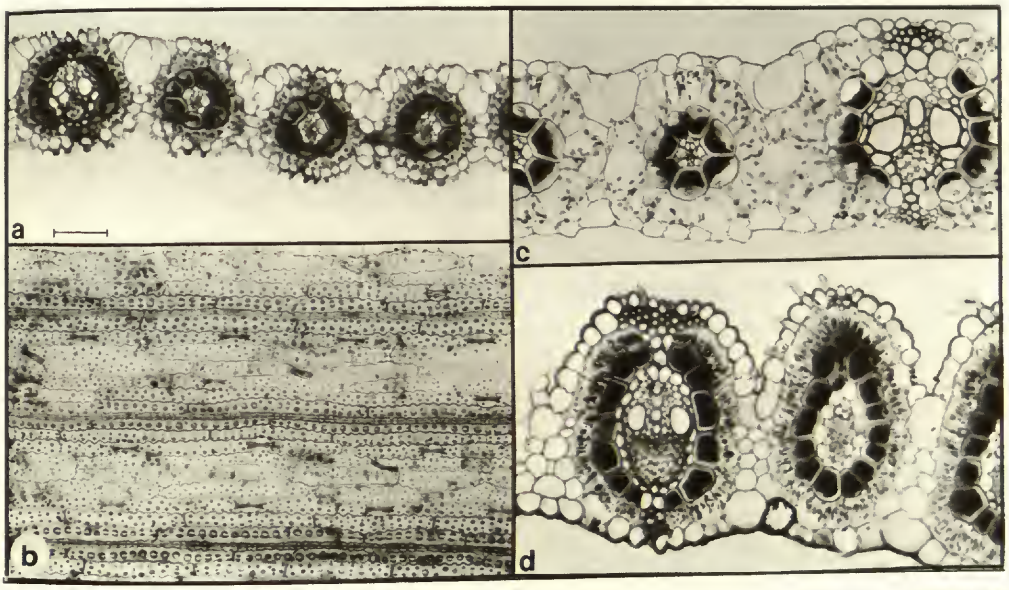

FIGURE 7. Group 3b, NAD-me C_4 *Panicum* species.—a, b. *P.* sp. aff. *P. repentellum, Ellis 3915*; a, transverse section showing NAD-me type anatomy with centripetal chloroplasts, but note adaxial and abaxial papillae; b, papillate abaxial epidermis.—c. *P. miliaceum, Ellis 3575,* with NAD-me type anatomy differing slightly from that of Group 3a.—d. *P. kalaharense, Ellis 3590,* with adaxial ribs and furrows. Scale = 50 μm.

anatomy are accommodated in this group. This group is consequently rather variable and no anatomical diagnosis can be given for the group as a whole. The anatomy of each species will therefore be discussed separately.

Included species:

Panicum arbusculum Mez. A species which undoubtedly belongs to the *P. coloratum* group but has been excluded here only because its leaf anatomy is specialized in having well-developed adaxial and abaxial ribs and furrows accompanied by sclerenchyma strands and girders which are not found in Group 3a. In all other respects the leaf anatomy of *P. arbusculum* compares favorably with that of *P. coloratum* and its allies. Morphologically it also differs from the Group 3a species in having woody culms and by forming large bushy tufts. Nevertheless, it seems best placed in the *Dichotomiflora* group and not in a miscellaneous group (Brown, 1977).

S.W.A. 2718: Grunau (CB), *Ellis 898.* CAPE. 2820: Augrabies Falls Natl. Park (CB), *Botha & Panagos 34*; Kakamas (DA), *Botha & Panagos 29.*

Panicum kalaharense Mez. (Fig. 7d). This species was not included in Group 3a because it has distinct adaxial ribs and furrows (Fig. 7d). This is virtually the only anatomical difference distinguishing *P. kalaharense* from the *P. coloratum* complex and, as the presence or absence of ribs and furrows may vary within genera (Clifford & Watson, 1977), this difference is considered of only specific diagnostic value. *P. kalaharense* is a member of the *Dichotomiflora* group (Brown, 1977) and this classification is supported by anatomical criteria.

CAPE. 2722: Olifantshoek (DC), *Botha & Panagos 43.*—2723: Kuruman (AD), *Ellis 3590.*

Panicum miliaceum L. (Fig. 7c). This species differs considerably from the *P. coloratum* group (Group 3a) in leaf anatomy. The individual vascular bundles are further apart (up to 100 μm), five or six minor bundles lie between successive first order vascular bundles, a large keel incorporating three large and six small bundles is present, the leaf blade is very wide (up to 20 mm) and thick (up to 200 μm). In epidermal structure there is a clear distinction between the long cells overlying the third order bundles and the true intercostal long cells, which is not the case in *P. coloratum.* The costal zones associated with the first order bundles are very widely spaced, only 3–5 cells wide, and have a single file of dumbbell- or cross-shaped silica bodies alternating regularly

with costal short cells. Anatomically, therefore, *P. miliaceum* is distinct from the *P. coloratum* assemblage. The classification of *P. miliaceum* in a separate section (or even subgenus) is supported by its leaf anatomy. *P. miliaceum* is not indigenous to southern Africa and is an annual weed of cultivation.

TRANSVAAL. 2528: Pretoria, cultivated (CA), *Ellis 3575, 4088.*

Panicum sp. aff. *P. repentellum* (Fig. 7a, b). This is the only indigenous southern African NAD-me *Panicum* species that does not belong to the *P. coloratum* complex. All specimens have very similar anatomy (Fig. 7a, b) that is clearly distinct from that of *P. coloratum*, the development of abaxial papillae being the most striking difference. The leaves are also much thinner (50–75 μm) and have fewer outer bundle sheath cells. Crenate intercostal silica bodies are also present.

The specimens included in this taxon are considered to be close to *P. repentellum*, which has been predicted to belong to the PEP-ck *Panicum* group (Group 2d) in this study. The correct identity of this taxon is, therefore, essential to a better understanding of both the PEP-ck species of Group 2d as well as the NAD-me species of Group 3. This is a hydrophytic grass which appears to be rare but widespread. A concerted effort should be made to gain a better understanding of the identity and relationships of this extremely interesting plant.

BOTSWANA. 1835: Chobe Natl. Park (DB), *Ellis 2918.*—2428: Warmbaths (CD), *Ellis 3915, 3916, 3917.*—2530: Belfast (CA), *Ellis 4438.*

Discussion. Panicum miliaceum appears to be the only representative of section *Panicum* in southern Africa. Material of *P. capillare* was also examined and compares favorably with *P. miliaceum*. This appears to confirm the sectional separation of *P. miliaceum* from the *Dichotomiflora* group, to which all the South African NAD-me *Panicum* species belong, except for the undescribed species close to *P. repentellum*.

Material of *Panicum racemosum* (Beauv.) Spreng and *P. urvilleanum*, both NAD-me species from Argentina, was also compared with this group. These two species belong to section *Dura* and differ considerably from sections *Panicum* and *Dichotomiflora*. This observation appears to strengthen the suggestion that several subgenera should be recognized in the genus *Panicum* even if it is reduced to only the NAD-me type species.

GROUP 4

No southern African species of *Panicum* have the NADP-me type of leaf anatomy that characterizes this group. These species only have a single bundle sheath (MS anatomy), which is Kranz with specialized chloroplasts usually centrifugally located (Ellis, 1977). This anatomy is unmistakable and easily recognized.

Panicum bulbosum H.B.K. was examined for comparative purposes (Fig. 8a–c). This comparison shows beyond doubt that no African *Panicum* species show any anatomical resemblances with these NADP-me *Panicum* species mainly from the New World. This applies to both leaf anatomy and epidermal structure.

GROUP 5

It has recently been discovered that intermediate C_3/C_4 species occur in *Panicum* with respect to both photosynthetic and anatomical attributes (Brown & Brown, 1975; Kanai & Kashiwagi, 1975; Morgan & Brown, 1979). Specimens of some of these intermediate species have been examined (Fig. 8d, e) to ascertain whether this anatomical type occurs in any southern African species. The anatomy of these species is Kranz-like in appearance, but with fewer chloroplasts in the outer bundle sheath cells and with the vascular bundles more widely spaced than in C_4 species. The proportion of the bundle sheath cell volume which is occupied by chloroplasts is considerably less in these C_3/C_4 intermediate species (Fig. 8d, e) than in any of the C_4 *Panicum* species. The lateral cell count (Hattersley & Watson, 1975) of the intermediate species varies between five and seven, whereas in the C_4 *Panicum* species it is two or four, and in C_3 species 7–10 mesophyll cells occur between successive vascular bundle sheaths. The leaf anatomy of these photosynthetically intermediate species is clearly intermediate between the C_3 and C_4 types and as such is readily recognizable. The epidermis of the species of this group is also distinct and does not resemble the C_3 type at all.

Species with intermediate anatomy and photosynthesis are only known from the *Laxa* group of the C_3 subgenus *Sarmentosum*. *Panicum decipiens* Nees ex Trin. (Fig. 8d), *P. milioides* Nees ex Trin., and *P. schenckii* Hack. (Fig. 8e) of this

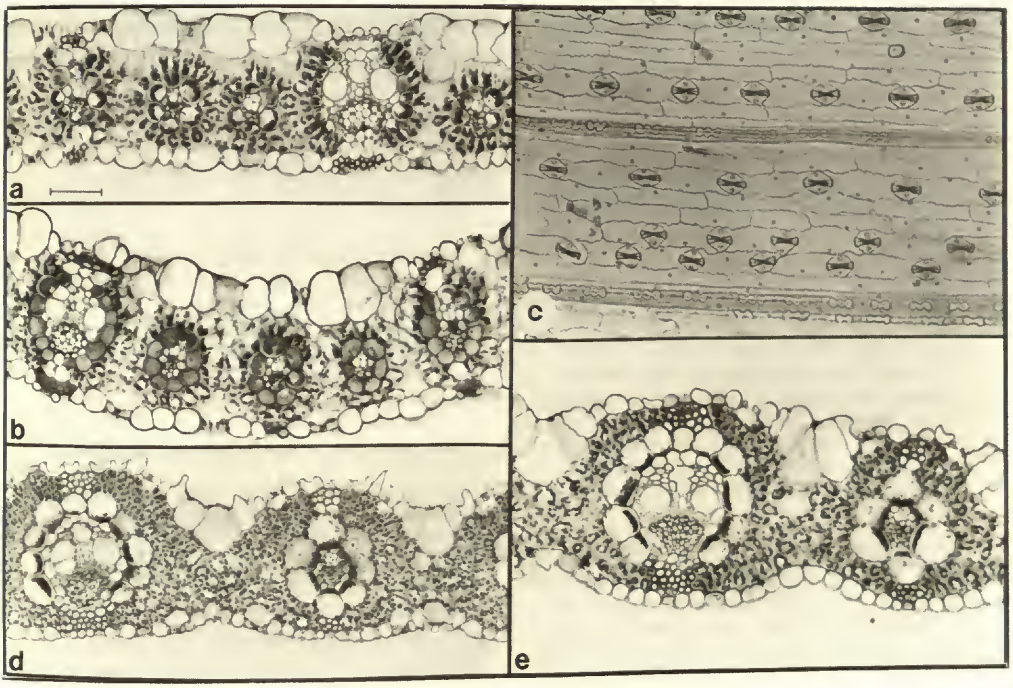

FIGURE 8. Anatomy of *Panicum* species belonging to Groups 4 and 5.—a–c. Group 4, *P. bulbosum* with NADP-me type anatomy, *Kew Garden No. 120-75.01349*; a, note single bundle sheath; b, with Kranz chloroplasts almost filling bundle sheath cells; c, abaxial epidermis with stomata, silica bodies and microhairs.—d, e. Group 5, anatomy of C_3/C_4 intermediate species; d, *P. decipiens, R. H. Brown 23*, with very few specialized centripetal chloroplasts and with lateral cell count greater than four; e, *P. schenckii, R. H. Brown 27*, with similar intermediate anatomy. Scale = 50 μm.

group have been shown to have intermediate photosynthesis and anatomy (Morgan & Brown, 1979; Wilson et al., 1983) and, together with several other species, have been raised to generic rank in *Steinchisma* (Brown, 1977). *Panicum hians* Ell. is also considered to be a C_3/C_4 intermediate (Hattersley, 1984). This species has been recorded in South Africa. Further collections are required in order to establish whether it is C_3/C_4 in this region.

C_3 species remain in the *Laxa* group, after removal of the intermediate species of *Steinchisma*. Several of these have been examined anatomically in this study but they do not resemble any of the C_3 *Panicum* groups from southern Africa. *Panicum hylaecium* Mez., *P. laxum* Sw., and *P. rivulare* Trin. all have air spaces reminiscent of the bambusoid fusoid cells, on either side of most vascular bundles. In epidermal structure they resemble the C_3/C_4 intermediate species closely. They differ from *Steinchisma* in habit, being mostly prostrate plants from partial or heavy shade and not erect plants from full sunlight.

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THE NERIEAE (APOCYNACEAE—APOCYNOIDEAE)

A. J. M. LEEUWENBERG[1]

ABSTRACT

The genera of tribe Nerieae of Apocynaceae are surveyed here and the relationships of the tribe within the family are evaluated. Recent monographic work in the tribe enabled the author to update taxonomic approaches since Pichon (1950) made the last survey. Original observations on the pollen morphology of the genera by S. Nilsson, Swedish Natural History Museum, Stockholm, are appended to this paper.

RÉSUMÉ

L'auteur étudie les genres de la tribu des Nerieae des Apocynacées et évalue les relations de la tribu au sein de la famille. Un travail monographique récent sur la tribu a permit à l'auteur de mettre à jour les approches taxonomiques depuis la dernière étude de Pichon (1950). Les observations inédites par S. Nilsson du Muséum d'Histoire Naturelle Suédois à Stockholm sur la morphologie des pollens des genres sont jointes à cet article.

The Apocynaceae have long been divided into two subfamilies, Plumerioideae and Apocynoideae (Echitoideae). Pichon (1947) added a third, the Cerberioideae, a segregate of Plumerioideae—a situation which I have provisionally accepted. These subfamilies were in turn divided into tribes and subtribes. Comparative studies have shown that the subdivision of the Plumerioideae is much more natural than that of the Apocynoideae.

Although the Apocynoideae is a coherent grouping, it has so far proved very difficult to devise a satisfactory and practicable subdivision for it. Pichon (1950) had little confidence in early classifications of the subfamily, although, like his predecessors, he seems to have preferred a more or less artificial treatment. He recognized four tribes in Apocynoideae—Echiteae, Nerieae, Apocyneae, and Ichnocarpeae—each of which was further divided into a number of subtribes. However, none of these can be maintained as delimited by Pichon. For example, there appears to be a greater degree of similarity between *Echites* and *Rhodocalyx* of the Echiteae and *Mandevilla* and *Mesechites* of the Ichnocarpeae than is evident from his classification.

Nevertheless, the Nerieae, dealt with in detail here, are maintained largely as proposed by Pichon except for the following changes: *Dewevrella* is transferred to Parsonsiineae (Echiteae). *Amphineurion* is treated as a synonym of *Aganosma*. De Candolle (1844) regarded *Amphineurion* as a section of *Aganosma*, but Pichon raised it to generic rank and in his arrangement included *Aganosma* in the Echitinae. Further, because of its conspicuous resemblance to *Beaumontia*, it may well be that *Amalocalyx* (Echiteae—Amalocalycinae, according to Pichon) ought to be moved to the Nerieae.

Pichon's system is artificial, because he used the shape and the indumentum of the area where the connectives cohere with the head of the pistil as the only character to distinguish the four tribes of his Apocynoideae. That the Nerieae is the most satisfactorily defined tribe of the Apocynoideae only becomes evident after combinations of characters are taken into account.

Pichon divided the Nerieae into nine subtribes (Table 1), but it is certain that not all of these can be maintained. Indeed, it is questionable whether the Nerieae ought to be divided into subtribes at all.

Connections can be seen between certain groups of genera. Thus *Adenium* has flowers that resemble those of *Nerium*, especially in the corona and in the long bristly appendages at the apices of the anthers.

Wrightia, *Pleioceras*, and *Stephanostema* can also be grouped together, as they have a corona (deeply incised in the first two and almost entire in the last one), more or less bifurcate ramification, and a similarly shaped corolla. There is, in addition, the resemblance shown by *Beaumontia* and *Vallaris* to *Wrightia*, in particular to those of its species with a broad corolla and thick-walled fruits. *Strophanthus*, with comparable

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TABLE 1. Pichon's treatment of the Nerieae compared with the arrangement proposed here.

Pichon (1950)	Leeuwenberg (1988)
Nerieae	Nerieae
1. Neriinae (as Amphineuriinae)	*Adenium* (5; Afr., Arab.; Plaizier, 1980)
Amphineurion (= *Aganosma*)	*Nerium* (1; Medit. to China; Leeuwenberg, 1984)
Pottsia	*Strophanthus* (38; Afr., As.; Beentje, 1982)
Dewevrella (to Parsonsiinae)	*Wrightia* (23; Afr., As.; Ngan, 1965)
Isonema	*Pleioceras* (5; Afr.; Barink, 1983)
Nerium	*Stephanostema* (1; Afr.; Barink, 1983)
2. Beaumontiinae	*Beaumontia* (9; As.; Rudjiman, 1986)
Vallaris	*Vallaris* (3; As.; Rudjiman, 1982)
Parabeaumontia (= *Vallaris*)	*Vallariopsis* (1; As.; Rudjiman, 1986)
Muantum (= *Beaumontia*)	*Kibatalia* (15; As.; Rudjiman, 1986)
Beaumontia	*Malouetia* (ca. 15; Afr., S. Amer.; Van der Ploeg, 1984, 1985; Fallen, unpubl.)
3. Strophantinae	*Allowoodsonia* (1; Pacif.; Fallen; unpubl.)
Christya (= *Strophanthus*)	*Funtumia* (2; Afr.; Zwetsloot, 1981)
Roupellina (= *Strophanthus*)	*Mascarenhasia* (ca. 10; Afr., Mad.; Markgraf, 1976)
Strophanthus	*Farquharia* (1; Afr.; Zwetsloot, 1981)
4. Mascarenhasiinae	*Alafia* (ca. 25; Afr., Mad.; Pichon, 1954)
Mascarenhasia	*Isonema* (3; Afr.; Van der Ploeg, 1983)
Echitella (= *Mascarenhasia*)	*Pottsia* (3; As.; Tsiang & Li, 1977)
5. Alafiinae	
Alafia	
Aladenia (= *Farquharia*)	
6. Kibataliinae	
Funtumia	
Kibatalia	
7. Wrightiinae	
Wrightia	
Wallida (= *Wrightia*)	
Scleranthera (= *Wrightia*)	
Pleioceras	
Stephanostema	
8. Malouetiinae	
Malouetia	
Malouetiella (= *Malouetia*) (Pichon, 1952)	
9. Adeniinae	
Adenium	
Vallariopsis not included.	
Allowoodsonia not mentioned.	

fruits and flowers with a corona, also belongs here.

A third group comprises *Kibatalia, Funtumia, Mascarenhasia, Malouetia,* and *Allowoodsonia.* These five genera probably all conform to the model of Koriba when in the flowering stage. *Funtumia,* however, matches the model of Prévost in the juvenile stage. This has still to be investigated for the other four genera. The coriaceous leaves, small stunted inflorescences, and fleshy corollas can make it difficult to distinguish these genera from each other. Within the group, *Malouetia* and *Allowoodsonia* are so close in all their characters, including those of the seeds (the only ones without a coma in the whole of the Apocynoideae), that the two should probably be united. *Kibatalia* differs from them only in the rostrum and coma of the seeds.

Farquharia and *Alafia,* large lianes with coriaceous leaves, exhibit similarity in their flowers and fruits, and they therefore form a fourth group within the Nerieae.

Of the three genera not yet mentioned, *Vallariopsis, Isonema,* and *Pottsia,* it is mainly *Vallariopsis* that shows connections with other genera. Thus, its flowers resemble those of *Kibatalia, Allowoodsonia,* and *Malouetia,* and to a lesser extent those of *Vallaris, Isonema,* and *Pottsia.*

The four groups outlined above could, if necessary, be distinguished as the subtribes Neriinae, Wrightiinae, Kibataliinae, and Alafiinae, but they are difficult to define.

Strophanthus gratus has flowers reminiscent of *Adenium* and *Nerium* in their corolla and corona. The corona and syncarpous fruits of *Nerium* have their counterparts in several *Wrightia* species. The model of Leeuwenberg has been recognized in species of *Nerium, Strophanthus boivinii,* and *Wrightia.* The seeds of *Beaumontia* resemble those of *Isonema* and *Pottsia.* In addition, the flowers of *Isonema* bear lateral appendages on the corolla lobes and, in this respect, are like those of *Mascarenhasia.* The remarkable long, slender, rostrate seeds of *Strophanthus,* with a coma on the rostrum, are also found in *Funtumia* and *Kibatalia.* On the other hand, the seeds of *Adenium* and *Farquharia* have basal and apical comas that are persistent, while in *Strophanthus, Funtumia,* and *Isonema* the second coma is deciduous.

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Appendix

Pollen Description of Apocynaceae–Apocynoideae–Nerieae[2]

Pollen grains usually spheroidal, 3(–4)-porate, exceptionally polypantoporate (*Vallariopsis*); exine smooth, perforated, often densely spaced towards the apertures; pores provided with thickened margin; inner exine consisting of globular or irregular elongated elements that are free or partly fused.

The exine fine structure varies among the taxa investigated with five or possibly six types:

(1) Exine stratified into tectum, a distinct central granular-columellate stratum and a basal stratum (sole, foot layer), endexine obsolete; the sole appears fragmented towards the pores (*Adenium obesum*). In *Vallaris solanacea* the granular stratum, when discernible, is displaced proximally towards the laminated sole.

(2) Exine with a relatively thick tectum, a distinct granular stratum more proximally located than in previous type, an unevenly thickened, partly discontinuous sole, fragmented near the apertures and possibly subtended by a thin, indistinct endexine (*Nerium oleander*).

(3) Exine stratified into tectum, a thin indistinct granular stratum subtended by a sole to which granules or knoblike elements are attached; near the apertures only granules (*Pleioceras barteri*).

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(4) Exine unstratified, with or without a central commissural line; inner face consists of small and large granules (*Farquharia elliptica, Funtumia africana, Kibatalia gitingensis, Mascarenhasia arborescens* var. *boivinii, Strophanthus gratus,* and *Wrightia pubescens*).

(5) Exine consists of an outer tectal stratum towards which free or fused rounded-elongated elements appear piled up (*Alafia lucida*).

The above arbitrary groups are not sharply delimited from each other, in particular group 4 from groups 3 and 5, respectively. From the complete exine in *Adenium* there is a series of transitional exine structures to the tectal-granular exine of *Alafia.*

Out of the remaining genera (pollen grains seen in LM or SEM only) it is only *Vallariopsis* that markedly deviates from all others by being poly-panto-porate. Pollen morphology does not reveal any evidence as to the position and interrelationships of *Allowoodsiana, Beaumontia, Isonema, Malouetia* (*Malouetiella*), *Pottsia,* and *Stephanostema.* Nor does it support the removal of *Amphineuron* and *Dewevrella* from the Nerieae.

Pollen morphologically, *Adenium* and *Nerium* appear related. *Wrightia* and *Strophanthus* appear related more to *Kibatalia, Funtamia, Mascarenhasia,* etc. than to *Pleioceras. Vallaris* shows certain similarity to *Adenium*; *Vallariopsis* is unique within the Nerieae. *Farquharia* appears closer to *Kibatalia, Funtumia,* etc., than to *Alafia.*

LES STRUCTURES REPRODUCTIVES DES MAGNOLIALES AFRICAINES ET MALGACHES: SIGNIFICATIONS PHYLOGENIQUES

A. Le Thomas[1]

Résumé

Caractéristiques des régions tropicales et tempérées chaudes, les Magnoliales sont particulièrement bien représentées en Afrique où, à l'exception des Magnoliacées, on trouve les Annonacées qui représentent à l'échelle mondiale les trois quarts de l'ordre, les Myristicacées, les Canellacées et, à Madagascar, les Winteracées. Pendant cette dernière décade, la compréhension de ces angiospermes primitives a beaucoup progressé grâce aux études palynologiques en microscopie électronique révélant certaines tendances évolutives de l'élément reproducteur mâle, et aux travaux concernant le mode de construction de la syncarpie dans ces groupes apocarpes. La comparaison de ces résultats avec les nombreuses informations acquises récemment sur les fossiles des premières angiospermes, en particulier sur les pollens, du Crétacé inférieur, confirme en grande partie l'unité des Magnoliales et la place privilégiée qui leur est souvent faite dans l'origine des angiospermes.

Abstract

Magnoliales, characteristic of tropical and warm temperate regions, are particularly well represented in Africa, where, with the exception of Magnoliaceae, one finds Annonaceae which represent three-fourths of the order on a worldwide scale, Myristicaceae, Canellaceae, and, in Madagascar, Winteraceae. During the last decade, our understanding of these primitive angiosperms has greatly increased thanks to palynological and electron microscopic studies that have revealed certain evolutionary tendencies of the male reproductive parts, and to work on the mode of construction of syncarpy in these apocarpous groups. The comparison of these results with numerous data recently obtained from fossils of the first angiosperms, in particular lower Cretaceous pollen, confirms in large part the unity of Magnoliales and the central place they are often accorded in the origin of the angiosperms.

Selon les auteurs et l'importance donnée à certains caractères morphologiques, l'ordre des Magnoliales renferme un nombre de familles variant entre sept et dix (Hutchinson, 1969; Cronquist, 1968, 1981; Takhtajan, 1973, 1980; Thorne, 1976; Walker, 1976; Dahlgren, 1980) et appartenant pour la plupart aux régions tropicales ou tempérées chaudes. Plusieurs petites familles monogénériques, ou même monospécifiques, telles que les Degeneriaceae, Himantandraceae, Eupomatiaceae, Austrobaileyaceae (Endress, 1980), sont strictement insulaires de la région Sud-Pacifique, tandis que les Winteraceae (Vink, 1970, 1977, 1978) également très répandues dans cette même aire géographique, sont représentées sur le continent sud-américain par trois espèces de *Drimys* et ont été découvertes à Madagascar en 1963 par Capuron (*Takhtajania* Baranova & Leroy, 1978). Beaucoup plus importante, la famille des Magnoliaceae est en grande partie restreinte à l'Asie du Sud-Est avec quelques espèces de *Magnolia*, *Talauma* et *Liriodendron* sur le continent américain, mais une discontinuité totale en Afrique.

Ainsi, à l'exception du *Takhtajania* malgache, les Magnoliales ne sont-elles représentées en Afrique que par trois familles mais non les moindres: deux d'entre elles sont pantropicales: les Annonaceae et les Myristicaceae, tandis que la petite famille des Canellaceae est restreinte à l'Amérique et l'Afrique.

L'idée que les Magnoliidae, et plus particulièrement les Magnoliales, sont des sortes de "fossiles vivants" angiospermiens est très largement répandue et assez généralement admise. En l'absence de données fossiles suffisantes, cette opinion s'est longtemps appuyée sur l'analyse morphologique comparative des plantes actuelles, mettant en évidence, chez les Magnoliales, un certain nombre de structures considérées comme primitives.

Ainsi, depuis les travaux de Thompson & Bailey (1916), considérant que la forme, la structure et l'arrangement des trachéides du bois de *Drimys*, *Tetracentron*, et *Trochodendron* étaient tout-à-fait comparables au bois des gymnospermes dépourvu de vaisseaux, cette structure est-elle très généralement considérée comme caractéris-

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tique des premières angiospermes (Dickison, 1975), même si le groupe gymnospermien ou progymnospermien auquel elles se rattachent reste encore très discuté (Doyle, 1978; Rettalack & Dilcher, 1981). Cependant, une analyse cladistique faite par Young (1981) conclut au caractère dérivé de l'absence de vaisseaux dans le bois des dicotylédones considérées jusqu'alors comme primitives. Il rejoint ainsi l'opinion de Jeffrey & Cole (1916), reprise en 1979 par Guédès qui exprimait ses doutes sur l'interprétation des caractères primitifs chez les "fossiles vivants." En outre, Young suggère que la condition primitive du bois des angiospermes s'exprimerait plutôt par la présence de vaisseaux à ponctuations scalariformes, tels que ceux que l'on trouve dans le genre *Austrobaileya*.

Les feuilles simples à marge entière, nervation pennée, nervures secondaires festonnées brochidodromes à eucamptodromes, nervures tertiaires irrégulières à régulières, stipulées à non stipulées sont représentatives des Magnoliales et reconnues comme primitives (Hickey & Wolfe, 1975). Bien qu'assez pauvres en types foliaires, les fossiles de la base du Crétacé inférieur étudiés par Hickey & Doyle (1977), renferment cependant quelques feuilles simples à pétiole peu différencié, marge entière et nervation brochidodrome, en mélange avec certains types monocotylédones. Sans être totalement décisives, ces données paléobotaniques récentes n'apportent cependant aucune contradiction à la notion primitive attribuée aux types foliaires des Magnoliales.

Le *pollen monosulqué* est sans doute le caractère magnoliacéen le plus généralement admis comme primitif chez les angiospermes (Wodehouse, 1935; Agababyan, 1973; Cronquist, 1981; Takhtajan, 1980; Walker, 1976; Le Thomas, 1978). Les données palynologiques fossiles (Muller, 1970) et, en particulier, celles du Crétacé inférieur (Doyle, 1969, 1977; Hickey & Doyle, 1977; Doyle et al., 1975, 1977, 1982; Walker & Walker, 1984) soutiennent actuellement très largement cette idée; cependant, elles ne paraissent pas encore suffisantes pour conclure que le pollen monosulqué dépourvu d'endexine, à exine très peu différenciée, du type Degeneriaceae (Dahl & Rowley, 1965; Walker & Skvarla, 1975), tel qu'il existe chez certaines Magnoliaceae (Praglowski, 1974) ou Annonaceae (Le Thomas & Lugardon, 1974, 1976a, 1976b; Walker, 1976) représente l'archétype du pollen des premières angiospermes.

Un autre concept, et peut-être le plus célèbre, dans l'évolution du système des angiospermes, est celui du *carpelle*. Sa nature morphologique et son évolution sont encore très controversées (Bailey & Swamy, 1951; Eames, 1961; Stebbins, 1974; Leinfellner, 1969b; Van Heel, 1981) par les morphologistes. Si dans ce domaine, les faits paléontologiques du Crétacé, bien que peu nombreux, suggèrent plusieurs lignées indépendantes dans l'évolution de la fleur des premières angiospermes (Dilcher, 1979), ils montrent cependant, que la plupart des spécimens du Crétacé inférieur ont des carpelles libres, condupliqués, à suture adaxiale, faiblement soudés, dès la limite supérieure de l'Albien. Bien que rapportées à d'autres types de structures florales que celles des Magnoliales, ces découvertes fossiles ne contredisent nullement la condition primitive de l'apocarpie. Elles suggèrent seulement que l'évolution vers la soudure des carpelles s'est développée très tôt (Dilcher, 1979), comme on peut le voir précisément dans certains groupes de Magnoliales.

Si les botanistes que nous sommes, constatent avec beaucoup d'intérêt les progrès accomplis pendant cette dernière décade par les paléobotanistes dans la connaissance des premières angiospermes du Crétacé, ils ont, pour leur part, acquis une quantité importante d'informations comparables, sur la structure du pollen et la structure carpellaire des Magnoliales qui demeurent encore, pour beaucoup d'entre eux, le terrain d'élection des premières angiospermes actuelles pour tenter d'expliquer leur évolution.

La Palynologie des Magnoliales Africaines

En Afrique, les Annonaceae sont, sans conteste, la famille la plus représentative des Magnoliales avec environ une quarantaine de genres, soit un tiers de la répartition mondiale et surtout la présence unique sur ce même continent des deux sous-familles et de toutes les tribus. J. Walker a, le premier (1971) donné un très large aperçu de la variation pollinique de cette famille dont on constate, après les études comparatives au microscope électronique par transmission (MeT), qu'elle traduit à elle seule une grande partie de celle du pollen des Magnoliales (Le Thomas, 1981). Les diversifications polliniques seront analysées sous deux aspects différents: la variation aperturale et la variation de la structure exinique.

Les résultats préliminaires sur la diversifica-

tion de l'aperture de l'ensemble des Annonaceae, dont l'étude avait été entreprise en collaboration avec G. Thanikaimoni, sont inclus dans cette analyse. L'observation critique des pollens turgescents traités par la méthode de Wodehouse et examinés au microscope photonique, a permis de mettre en évidence la présence d'apertures dans de nombreux cas considérés jusqu'à présent comme inaperturés. D'autre part, l'examen de la polarité au stade tétrade, ainsi que la répartition de l'intine, ont révélé la présence de nouveaux types de pollens non signalés auparavant.

LES APERTURES

Le type d'aperture le plus commun dans le pollen des Magnoliales est le type *monosulqué*, présent dans presque toutes les familles et parfois de façon exclusive, à l'exception des Eupomatiaceae et Winteraceae, si l'on accepte la plus large définition de l'ordre (Cronquist, 1981). Un consensus général paraît actuellement réalisé pour admettre que ce type pollinique représente le type primitif des angiospermes (Doyle, 1969, 1978; Muller, 1970; Doyle et al., 1975; Hickey & Doyle, 1977; Walker & Walker, 1984). De nombreux arguments viennent étayer cette hypothèse: la fréquence de ce type pollinique dans plusieurs groupes de gymnospermes actuels et fossiles, sa répartition parmi les fossiles d'angiospermes les plus anciens au Crétacé inférieur (monocotylédones ou dicotylédones) et sa persistance dans les monocotylédones actuelles comme dans certains groupes de dicotylédones à caractères primitifs.

En Afrique, ce type pollinique est bien représenté dans les Annonaceae (Le Thomas, 1981) où il est comparable par sa forme elliptique allongée au pollen des Magnoliaceae et Degeneriaceae, tandis que le pollen sulqué des Canellaceae (Wilson, 1964) et Myristicaceae (Walker & Walker, 1980, 1981) est plus sphérique comme chez certaines autres Annonaceae ou chez les Himantandraceae (Walker, 1976).

A partir de ce type de base (Fig. 1a), on retrouve dans les Annonaceae africaines la presque totalité des types polliniques actuellement connus dans la famille, ce qui permet d'établir les différentes tendances de l'évolution des apertures.

1. *Conservation du sillon distal.* Une première tendance s'exprime dans la conservation d'un véritable sillon distal, mais l'association des monades sulquées conduit à un type de tétrade monosulquée (Fig. 1b), dans lequel l'exine non aperturale est régulièrement répartie autour de chaque grain individuel. C'est le cas du genre américain *Pseudoxandra* (Walker, 1971; Le Thomas et al., 1986). Ce type pollinique est absent en Afrique. A Madagascar, il existe un type de pollen sulqué (Fig. 1c), particulièrement original, par sa forme conico-convexe très dissymétrique, dans le genre *Ambavia* (Le Thomas, 1972). Peut-être peut-on imaginer que ce type monosulqué, à exine proximale très amincie, soit le résultat d'une prolongation du stade tétrade à monades monosulquées, dont il dériverait, le développement normal des parois proximales ayant été empêché. Si les types polliniques de cette première lignée évolutive sont différents, ils n'offrent en réalité aucune variation dans le type apertural qui demeure sulqué distal.

2. *Acquisition d'opercule, suivi d'un déplacement et extension de l'aperture vers l'équateur.* Cette lignée évolutive correspond à la tendance II décrite par Muller (1970) dans son schéma de l'évolution de l'aperture du pollen des angiospermes. La première étape de transition qui consiste en *l'acquisition d'un large opercule* couvrant l'aperture distale, sauf au niveau des marges (Fig. 1d), n'a pas encore été rencontré dans les genres africains, mais est présente dans le genre américain *Bocageopsis* (Waha, 1985; Le Thomas & Thanikaimoni, 1987). Par perte de l'intine en-dessous de l'opercule, restreignant ainsi la région aperturale à une ceinture subéquatoriale ou équatoriale, on aboutit à un type pollinique dont l'aperture est *continue équatoriale*, comme chez *Letestudoxa* et *Pseudartabotrys* (Fig. 1e). Le type monosulqué operculé peut également se diversifier par soudure des extrémités de l'opercule avec la partie non aperturale et, dans ce cas, aboutir à un type *sulqué pontoperculé* (Fig. 1f) comme dans *Enantia* ou dans le genre asiatique *Alphonsea* (Le Thomas & Thanikaimoni, 1987). Dans les deux types operculés, le pollen montre une asymétrie, non seulement dans la partie exinique, mais aussi dans la répartition de l'épaississement de l'intine.

Le pollen de *Sapranthus* a été décrit comme disulqué avec deux apertures plus ou moins équatoriales par Walker (1971) et disulqué avec deux apertures polaires, l'une distale, l'autre proximale (Waha & Hesse, 1988; Le Thomas & Thanikaimoni, 1987). La polarité de l'aperture dans le stade tétrade n'a pu encore être établie faute de matériel suffisamment jeune. Cependant, si l'on tient compte de la répartition de

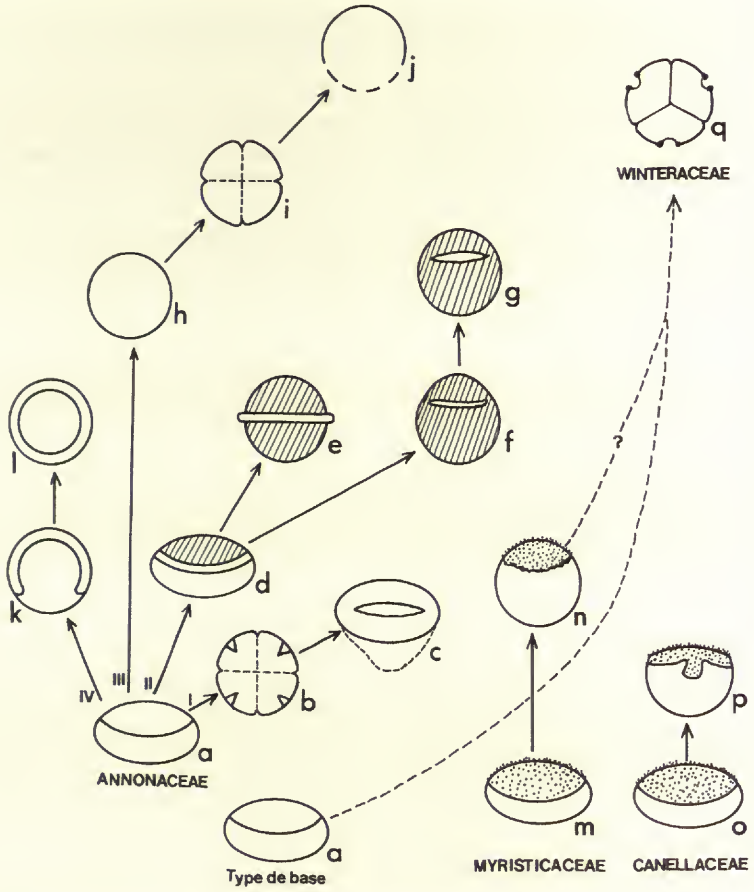

FIGURE 1. Diversification aperturale des pollens des Magnoliales africaines.

l'intine, il aparaît qu'il s'agit en effet de deux apertures distales.

A partir du type sulqué pontoperculé, une restriction de l'aperture, seulement dans les parties marginales, par réduction de l'intine au-dessous du pontopercule, conduit en effet au type *disulqué* (Fig. 1g), tel qu'on le trouve aussi dans le genre africain *Afroguatteria* (Le Thomas & Thanikaimoni, 1987). Il s'agit d'un pollen à deux apertures distales, parallèles à l'équateur, séparées par une région non aperturale proximale. Le type dicolpé équatorial, signalé comme l'un des points culminants de la tendance III de Muller, est comparable au type disulqué d'*Afroguatteria*, mais semble dérivé, chez les Annonaceae, du type pontoperculé qui pourrait représenter une étape intermédiaire entre les tendances II et IV de Muller.

3. *Perte de l'aperture.* Cette troisième tendance aperturale des Annonaceae correspond au point de départ de la lignée III de Muller. Elle se manifeste par un manque de différenciation entre la partie aperturale et non aperturale, aboutissant à un type *simple inaperturé* (omniaperturé de Thanikaimoni, 1978), comme dans le genre *Friesodielsia* (Fig. 1h). Dans ce cas, la polarité ne peut être reconnue dans le sporoderme, ce qui explique que ce type ait parfois été décrit comme apolaire (Walker, 1971). La prolongation du stade tétrade au stade adulte de ce type inaperturé conduit à un type de *tétrades inaperturées* (ou polyades). Très fréquent en Afrique (Fig. 1i), comme dans *Asteranthe* par exemple, ce type est caractérisé par un important amincissement de l'exine en région proximale (Guinet & Le Thomas, 1973), sans que l'intine

ne soit modifiée. Lorsque l'association des monades est particulièrement faible, elles se séparent et donnent naissance à un autre type pollinique *simple inaperturé à amincissement exinique proximal* (Fig. 1j) tel qu'on le rencontre dans le genre *Isolona* (Le Thomas et al., 1986).

Il est intéressant de souligner que dans les tendances 1 (sulquée) et 3 (inaperturée), on retrouve des étapes comparables dans l'association des monades en tétrades, et l'aboutissement aux monades à amincissement proximal.

4. *Extension méridienne de l'aperture* (à établir). A partir du type sulqué de base, on observe une autre tendance qui, par extension méridionale de l'aperture (Fig. 1k) conduit à un type sulqué étendu dont l'extrémité se trouve dans la région proximale. L'extension de cette aperture jusqu'à la soudure des extrémités au pôle proximal, aboutit à une *ceinture méridienne aperturale* (Fig. 1l). Ces deux étapes d'évolution devraient être cherchées parmi les genres à aperture ceinturale comme peut-être le genre asiatique *Desmos*. Cette lignée évolutive correspond, en partie, à la tendance IV du schéma de Muller.

Ainsi, la diversification de l'aperture du pollen des Annonaceae se traduit actuellement par 12 types de pollens représentant quatre principales tendances évolutives, mais chaque investigation nouvelle au MeT montre la complexité palynologique de cette vaste famille, tant dans l'interprétation aperturale que dans son évolution.

Chez les Myristicaceae le type de base est également monosulqué (Fig. 1m) mais l'aperture est recouverte d'une membrane plus ou moins verruqueuse ou grossièrement granuleuse et ses marges non diffuses sont brusquement marquées par des agglomérations de gros granules. Ce type est présent dans les genres africains: *Coelocaryon klainii* (Walker & Walker, 1980, fig. 5) et malgaches: *Mauloutchia coriacea* (Walker & Walker, 1981, fig. 6).

Dans un deuxième stade, on observe un début de *réduction de la surface aperturale* (Fig. 1n; Walker & Walker, 1980, fig. 19) qui pourrait être liée à la forme plus ou moins pyriforme ou ellipsoïde du pollen dont le contour distal est plus ou moins circulaire, tel qu'il apparaît dans le genre *Scypocephalium* (Walker & Walker, 1980, fig. 22) ou *Mauloutchia chapelieri* (Walker & Walker, 1981, fig. 5). Dans ce cas, l'aperture devient plus ou moins circulaire, mais elle est trop grande pour être appelée *ulcus*.

Erdtman (1952) définit en effet l'ulcus comme une aperture restreinte au pôle distal, tandis que le type ulcéré des Myristicaceae (Walker & Walker, 1980) occupe une aire beaucoup plus vaste. Ce type d'aperture ne serait-il pas plutôt une simple variation du sulcus et un type de passage vers l'ulcus?

Beaucoup moins diversifiée que chez les Annonaceae, la tendance évolutive aperturale du pollen des Myristicaceae africaines correspond, dans une certaine mesure, au premier stade de la tendance II de Muller, sans toutefois atteindre le type ulcéré (ou monoporé).

Chez les Canellaceae le type de base est encore monosulqué (Fig. 1o). La seule variation qui existe dans le genre est-africain, *Warburgia*, est le contour trichotome de l'aperture (trichotomosulcus) (Fig. 1p), également présent dans les genres américains (Wilson, 1964; Walker, 1974, 1976). La membrane aperturale est toujours recouverte d'éléments plus ou moins granuleux ou verruqueux. Il s'agit donc d'une famille dont le pollen semble avoir très peu évolué sur le plan apertural. Il correspond d'ailleurs à la première étape de la tendance I de Muller.

Chez les Winteraceae on ne trouve pas le type de base monosulqué, mais seulement des pollens en tétrades à surface aperturale réduite et de contour irrégulier (Fig. 1q). Décrite comme un pore, l'aperture correspond en réalité à un ulcus puisqu'elle est distale. Dans le seul genre malgache, *Takhtajania*, l'aperture est entourée d'une marge nette recouvrant un épaississement endexinique important ou costa. La membrane aperturale est verruqueuse ou clavée (Lobreau-Callen, 1977; Pragloswki, 1979). Il faut également mentionner l'amincissement de l'exine proximale liée à la cohésion des monades. Ce type apertural a été considéré comme le premier stade de la tendance II de Muller, mais il comporte une aperture complexe et non simple.

Ainsi, dans les trois principales familles de Magnoliales africano-malgaches, on retrouve le type pollinique monosulqué primitif qui peut traduire un lien phylogénique très ancien entre elles. Cependant, on constate qu'il n'évolue que très peu chez les Myristicaceae et Canellaceae, alors qu'il montre une large diversification chez les Annonaceae. Sans représentant monosulqué, mais avec une unique aperture distale, le pollen des Winteraceae pourrait encore représenter un stade peu avancé dans l'évolution aperturale, mais la complexité de son aperture (annulus et costae) l'isole pourtant nettement dans le schéma des Magnoliales africaines. Il paraît à cet égard

constituer plutôt une fin de phylum qu'un début d'évolution.

STRUCTURE DU SPORODERME

L'ultrastructure du sporoderme des pollens de l'ensemble des Magnoliales n'est pas encore totalement étudiée mais ces dernières années ont fait considérablement progresser notre connaissance dans ce domaine, et en particulier pour les groupes présents en Afrique.

1. *L'endexine.* Dans leur très grande majorité, les pollens de Magnoliales semblent caractérisés par *l'absence d'endexine,* à l'exception des Austrobaileyaceae (Endress & Honegger, 1980) et des Winteraceae (Lobreau-Callen, 1977; Praglowski, 1979). Chez les Canellaceae, elle est toutefois signalée sous l'aperture (Walker, 1976). Dans toutes les autres familles et, en particulier dans les Magnoliaceae (Roland, 1968; Praglowski, 1979), Annonaceae (Le Thomas & Lugardon, 1972–1977; Le Thomas, 1981), et Myristicaceae (Walker & Walker, 1980, 1981), l'endexine est totalement absente, quel que soit le type pollinique ou le type de structure ectexinique. Ainsi, la présence d'endexine dans le pollen du genre *Takhtajania* accentue-t-elle encore son caractère original comparativement au pollen des autres Magnoliales africano-malgaches.

2. *La couche basale.* Parmi les Magnoliales africaines, et probablement l'ensemble de l'ordre, c'est le pollen des Annonaceae qui offre la plus grande variation à ce niveau. Certains pollens sulqués, tels que celui de *Piptostigma,* ou inaperturés échinulés, tels que celui de *Friesodielsia* (Le Thomas & Lugardon, 1974) ont une *exine totalement dépourvue de couche basale.* En Afrique, ce type d'exine ne se rencontre que chez les Annonaceae, mais il est également caractéristique des Degeneriaceae, Himantandraceae et Eupomatiaceae (Walker & Skvarla, 1975).

Décrite pour la première fois dans l'ectexine des Annonaceae, la *structure feuilletée lamellaire* de la couche basale (Le Thomas & Lugardon, 1974) est aussi particulièrement caractéristique de cette famille dans laquelle elle peut être associée à tous les types de structures exiniques et présente dans tous les types polliniques. Parfois réduite à quelques feuillets très fins et discontinus, dans les pollens simples, elle peut aussi prendre une grande extension comme chez *Uvaria* et plus généralement dans les tétrades où, lorsqu'elle existe, elle constitue le seul lien exinique qui unit les monades en région proximale (Le Thomas & Lugardon, 1972). Dans certains cas, les feuillets ne constituent que la partie interne de la couche basale épaisse et homogène dans sa partie externe, comme dans l'espèce malgache *Polyalthia capuronii* (Le Thomas & Lugardon, 1976b).

Cette couche ectexinique feuilletée lamellaire est inconnue dans le pollen des Canellaceae et des Winteraceae qui ont une couche basale homogène, mais elle a fréquemment été mise en évidence par Walker & Walker (1980, 1981, 1984) dans les Myristicaceae et spécialement dans les genres africano-malgaches. Egalement associée aux divers types de structures ectexiniques, elle peut y être totalement lamellaire comme chez *Mauloutchia parvifolia,* mais le plus souvent, elle ne constitue que la partie interne de la couche basale, par ailleurs épaisse et homogène dans sa partie externe (*Cephalosphaera*). Ce type de couche basale rappelle beaucoup celui des Magnoliaceae (Praglowski, 1974).

3. *La couche infratectale.* Classiquement décrite comme couche columellaire dans le pollen des angiospermes, jusqu'à ce qu'on y ait reconnu un nouveau type de structure constituée de grains (Van Campo & Lugardon, 1973), cette couche correspond à ce que Walker & Walker (1981) appellent "interstitium." Ce terme décrit ainsi la partie exinique comprise entre le tectum et la nexine ou couche basale, quelle que soit sa nature.

C'est encore dans le pollen des Annonaceae qu'on trouve la plus grande diversification de cette couche ectexinique, sa structure pouvant être grenue, columellaire, ou présenter de nombreuses formes intermédiaires. Très fréquente, la *structure grenue* peut y présenter un aspect particulièrement peu différencié, dans lequel les grains sont trop petits pour être observés au microscope optique, au point même de donner à l'exine une apparence presque homogène et atectée (Walker, 1974). Ce type d'exine se rencontre chez certains pollens sulqués, tels que *Piptostigma* (Van Campo & Lugardon, 1973; Le Thomas & Lugardon, 1974), et devient tout-à-fait comparable à celui des Degeneriaceae (Dahl & Rowley, 1965; Walker & Skvarla, 1975) dans lequel la couche basale est également absente. Chez les Annonaceae, il est encore présent dans les pollens inaperturés échinulés comme celui de *Friesodielsia,* mais il n'est signalé, jusqu'à présent dans aucune autre Magnoliale africaine.

La diversification de cette couche infratectale

grenue est particulièrement intéressante dans les Annonaceae africaines où il a été possible de montrer de très nombreux intermédiaires entre le grain et la columelle, parfois même dans un seul genre comme *Polyalthia* (Le Thomas & Lugardon, 1976b). Une série structurale comparable a également été observée chez les Myristicaceae malgaches (Walker & Walker, 1980) dans le genre *Mauloutchia,* où l'exine à grains plus ou moins organisés radialement constitue un terme de passage entre les espèces dont le pollen présente une couche grenue à grains non orientés (*M. heckelii, M. chapelieri*) et celles dont la couche infratectale est columellaire (*M. coriacea*).

L'ultrastructure de l'exine du pollen des Canellaceae africaines et malgaches n'a pas encore été étudiée, mais on sait qu'il existe dans la famille des structures grenues et columellaires et des grains en mélange avec la columelle dans le genre américain *Pleodendron* (Walker, 1974). Par ailleurs, le pollen fovéolé du genre africain *Warburgia* est considéré comme le plus proche des types comparables chez les Magnoliaceae et Degeneriaceae (Walker, 1976).

Chez les Winteraceae, en revanche, la couche infratectale n'est jamais grenue, mais toujours constituée de columelles bien développées (Praglowski, 1979) et le pollen du genre *Takhtajania* ne fait pas exception à la règle (Lobreau-Callen, 1977).

4. *Le tectum.* On a pu montrer, dans le pollen des Annonaceae africaines, que la surface tectale était directement liée à la structure exinique et paraissait traduire l'évolution de l'ectexine (Le Thomas, 1981).

Aux types d'exine à structure infratectale grenue, le plus souvent dépourvue de couche basale feuilletée lamellaire, à l'exception du pollen d'*Uvaria,* correspond généralement un tectum lisse, continu, microperforé, les perforations circulaires et étroites étant irrégulièrement réparties et peu nombreuses (*Lettowianthus, Cananga*). Ce type de tectum (tecté-imperforé de Walker) se retrouve également dans les pollens de certaines Canellaceae telles que *Warburgia* ou Myristicaceae comme *Brochoneura* où la couche infratectale de l'exine est également constituée de grains.

Tandis que les Winteraceae ont toujours un tectum réticulé, le pollen des Myristicaceae et Annonaceae africaines présente une variation de la surface tectale très diversifiée et souvent comparable (Le Thomas, 1981; Walker & Walker, 1980, 1981). Ils ont en commun des surfaces tectales échinulées, associées à une structure ectexinique grenue peu différenciée et correspondant à un stade évolutif peu avancé (*Friesodielsia, Mauloutchia heckelii*). Cependant, les Myristicaceae africaines offrent, dans le genre *Pycnanthus,* un autre type d'exine échinulée, beaucoup plus évolué, puisque les épines sont supratectales, le tectum étant finement réticulé et la couche infratectale columellaire.

Dans ces deux familles, les surfaces granuleuses ou verruqueuses d'aspects variés, mais toujours très discontinues, sont également fréquentes, surtout lorsque l'exine a une structure infratectale grenue désordonnée (*Uvariopsis congensis, Mauloutchia humblotii*). On y observe la même tendance à l'allongement des éléments tectaux, de plus en plus soudés, constituant un tectum verruqueux-rugulé (*Isolona hexaloba, Mauloutchia chapelieri*), aréolé-rugulé, à rugulé-perforé (*Mauloutchia coriacea, Uvariopsis congolana*), rugulé-réticulé (*Haematodendron glabrum, Uvariodendron molundense*), de moins en moins discontinu dans les pollens à exine columellaire. Chez les Annonaceae, il peut même devenir lisse-perforé (*Enantia chlorantha*) et dans ce cas il est toujours associé à une structure infractectale columellaire. Ce type de tectum est également présent dans les Canellaceae (Walker, 1974). L'élargissement de ces perforations conduit à une série microréticulée-réticulée dans le genre *Annona* dont on trouve certaines étapes chez les Myristicaceae (*Pycnanthus, Coelocaryon*).

Les exines intectées que l'on peut observer dans les Annonaceae, soit sous forme d'éléments libres clavés, comme chez *Ophypetalum* ou seulement constituées de feuillets lamellaires, comme chez *Toussaintia,* sont absentes dans le pollen des Myristicaceae. En revanche, le type de surface crotonoïde que l'on rencontre dans le genre *Scyphocephalium* est inexistant dans les Annonaceae. En dépit de ces quelques exceptions, on observe dans ces deux familles de Magnoliales africaines le même type de variation tectale qui semble traduire également celle de la structure exinique.

S'il existe un consensus général sur le type pollinique primitif des angiospermes, monosulqué ellipsoïde allongé, tel qu'on le trouve dans les Annonaceae et Magnoliaceae, il est, en revanche, impossible de s'appuyer sur les données paléontologiques actuelles pour déterminer le type de structure exinique le plus ancien dans les Magnoliales actuelles. Le seul moyen pour avancer une hypothèse dans ce domaine est donc encore de faire appel à l'analyse comparative des différents

caractères morphologiques, dans une même famille, afin d'éviter l'interprétation de formes de convergence.

En raison de leur large diversification, les Annonaceae africano-malgaches sont particulièrement significatives. Les corrélations de caractères autorisent alors à déduire que la structure columellaire est dérivée (Le Thomas, 1981). Ainsi, dans une même série structurale (*Polyalthia*), le pollen monosulqué tecté microperforé, à structure infratectale grenue peu différenciée, dépourvue de couche basale et d'endexine, devient le type de base de la famille, à partir duquel se différencie la structure columellaire. Ce type de pollen n'est connu, jusqu'à présent, que chez les Degeneriaceae (Walker & Skvarla, 1975) et les Annonaceae, dans le genre africain *Piptostigma* (Le Thomas & Lugardon, 1974). Par comparaison, la structure exinique du pollen des Magnoliaceae semble plus évoluée, puisqu'elle est toujours tripartite. C'est également le cas des exines de Myristicaceae qui présentent cependant une variation structurale très comparable à celles des Annonaceae, alors que la diversification aperturale est beaucoup plus réduite, et la forme du pollen moins allongée. Il est en de même pour le pollen des Canellaceae, dont on ignore cependant l'ultrastructure exinique, dans le genre africain *Warburgia* qui par son tectum lisse rappelle beaucoup le type pollinique de *Degeneria*. Il se pourrait fort bien qu'au MeT, la couche ectexinique continue, observée en photonique par Wilson (1964) présente également une structure grenue très peu différenciée. Toutefois, l'endexine a été signalée, au moins sous l'aperture.

Si les Annonaceae apparaissent beaucoup plus diversifiées sur le plan palynologique, le pollen des Myristicaceae, comme celui des Canellaceae, établit des liens très étroits entre ces trois familles de Magnoliales présentes en Afrique. Il confirme leur rapprochement déjà suggéré par plusieurs auteurs (Walker, 1971; Cronquist, 1981), mais aussi leur place parmi les Magnoliales.

En revanche, le pollen de *Takhtajania*, comme celui des autres Winteraceae, apparaît comme une sorte d'anomalie au sein des Magnoliales africano-malgaches. Isolé par son type pollinique, il l'est encore bien davantage par ses apertures complexes et sa structure exinique columellaire à couche basale homogène et endexine bien développée. Ces caractères polliniques très anciens, puisqu'ils ont été retrouvés dès l'Aptien (Walker et al., 1983), témoignent sans doute d'une évolution déjà bien avancée à cette époque où la plupart des types polliniques étaient diversifiés, mais ils n'indiquent pas pour cela de lien direct avec les Magnoliales.

Les Structures Carpellaires des Magnoliales Africaines

A la suite des travaux de l'école de Bailey, il est encore souvent admis que le carpelle des angiospermes est fondamentalement condupliqué, les ovules étant situés sur la face adaxiale (ventrale). Cette notion est contestée par certains arguments tératologiques et histogénétiques (Rohweder, 1959; Guédès, 1966) et ne semble pas s'appliquer aux Magnoliales. En effet, Leinfellner (1966–1969) a montré que les carpelles des Magnoliales sont généralement peltés, leurs marges étant unies congénitalement dans la région inférieure; ils ne sont condupliqués qu'au niveau de leur fente ventrale qui est la zone ovulaire. Les observations de Guédès (1968) sur le carpelle de *Liriodendron tulipifera*, confirment ces conclusions sur la morphologie peltée (ascidiée) du carpelle des Magnoliales. Plus récemment, Endress (1980–1983) a réexaminé la structure florale d'*Austrobaileya* et montré que les carpelles étaient très fortement ascidiés, l'ascidiation s'étendant même à la plus grande partie du style, et les ovules étant tous insérés ventralement dans la région congénitalement close.

Enfin, l'ontogénie des carpelles libres représentatifs d'une vingtaine de familles et observée au MeB par Van Heel (1981, 1983), indique qu'à partir d'un méristème circulaire ou convexe, ils se développent tous en une structure oblique ascidiée, l'apparence condupliquée n'étant atteinte qu'à un stade ultérieur. Comme pour Leinfellner (1969b), la structure peltée ou ascidiée représenterait pour Van Heel la forme originelle du carpelle des angiospermes.

Les carpelles libres

Seules les Annonaceae et les Myristicaceae possèdent des carpelles libres parmi les Magnoliales africaines, la seule Winteraceae malgache ayant un ovaire syncarpe (Leroy, 1977; Vink, 1978).

A l'exception de deux études faites sur les carpelles de *Cananga* (Periasay & Swamy, 1956) et de *Polyalthia* (Padmanabhan, 1968), l'anatomie des carpelles libres d'Annonaceae n'a guère retenu l'attention. Cependant Leinfellner (1969b)

considère que, dans la plupart des cas, les carpelles ne sont pas peltés, n'ayant pas de zone ascidiée basale, à la différence des Winteraceae et Magnoliaceae (Tucker, 1959; Sampson & Tucker, 1978). Toutefois, l'observation d'un pédoncule unifacial à faisceaux ventraux soudés l'un à l'autre, chez *Polyalthia* et *Uvaria,* entraîne Leinfellner à penser que le carpelle non pelté des Annonaceae pourrait provenir d'un carpelle ascidié. Des études anatomiques actuellement en cours sur plusieurs genres d'Annonaceae montrent en effet que les carpelles d'*Anaxagorea* ont une zone ascidiée basale très courte dans laquelle on ne peut distinguer aucune ligne de suture carpellaire au-dessous de la cavité ovarienne fertile à marges non soudées (Deroin, communic. pers.). Ceci tendrait à confirmer l'origine carpellaire des Annonaceae à partir d'un carpelle ascidié (Van Heel, 1981) tout en renforçant les liens déjà très étroits établis par Endress (1980) entre les Austrobaileyaceae et les Annonaceae dans lesquels les stigmates sont également très souvent papilleux (Le Thomas, 1969) et secréteurs (Gottsberger, 1970).

Chez les Myristicaceae, le carpelle est unique (Sastri, 1959) bien que la présence du stigmate bilobé ait pu conduire certains auteurs à en déduire celle de deux carpelles (Nair & Bahl, 1956). Leinfellner considère pour sa part que le gynécée des Myristicaceae est tout-à-fait comparable à celui de certaines Annonaceae, sans véritable zone basale ascidiée mais probablement avec un pétiole carpellaire unifacial.

Ainsi, dans ces deux familles de Magnoliales africaines, on ne trouve pas de véritable structure ascidiée du carpelle, comme chez les Magnoliaceae, Winteraceae ou Austrobaileyaceae, mais un résidu d'ascidiation à la base du carpelle qui peut totalement disparaître chez les Annonaceae.

LES OVAIRES COMPOSÉS: SYNCARPIE

Une des étapes fondamentales dans l'évolution des angiospermes est l'acquisition de la syncarpie qui caractérise la plus grande partie des plantes à fleurs. Endress (1982) a analysé et synthétisé les avantages de cette structure comparée à l'apocarpie des angiospermes primitives et souligné, entre autres, l'intérêt fonctionnel de la fusion carpellaire dans le fruit. Cette fusion postflorale est rare, mais se rencontre chez les Annonaceae (pseudosyncarpie; Le Thomas, 1981). Dans les Magnoliales, la vraie syncarpie est rarement réalisée à l'exception du gynécée des Monodoroideae, sous-famille africano-malgache des Annonaceae, des Canellaceae et des Winteraceae (*Takhtajania* malgache).

Chez les Annonaceae, la syncarpie a été très tôt reconnue par Dunal (1817) et partiellement démontrée par Baillon (1869) qui décrivait l'ovaire comme uniloculaire, à nombreux placentas pariétaux, les ovules "paraissant primitivement disposés sur chaque placenta suivant deux séries parallèles et se tournant le dos." A la suite d'une étude organogénétique de *Monodora crispata,* Leins & Erbar (1979) ont remis en cause cette syncarpie des Annonaceae, généralement acceptée par les systématiciens et les morphologistes (Leinfellner, 1969b), pour conclure à la monocarpellie du gynécée, tout en lui conférant une placentation laminale d'un type unique chez les dicotylédones.

L'étude de la vascularisation du gynécée de la fleur épanouie de *Monodora crispata* (Guédès & Le Thomas, 1981), ainsi que celle de plusieurs autres espèces de *Monodora* et d'*Isolona campanulata* (Deroin, 1985), appuie au contraire la théorie classique du gynécée syncarpe uniloculaire. Quel que soit le nombre de carpelles qui le compose (6–14), la structure du gynécée des Monodoroideae est très semblable et la vascularisation montre que la syncarpie avec union congénitale des carpelles y est déjà très avancée, chaque carpelle étant séparément non ascidié. La présence de faisceaux latéraux confirme l'interprétation des faisceaux principaux comme étant les faisceaux médians carpellaires, ce qui explique la disposition des ovules apparemment adossés. En réalité, cette interprétation ne paraît nullement contradictoire avec les observations de Leins & Erbar (1979) selon lesquelles le gynécée apparaît ontogénétiquement constituer une unité dans laquelle les carpelles sont indiscernables extérieurement. En revanche elle a l'avantage d'expliquer la disposition des ovules et de montrer qu'elle est pariétale comme dans les autres Magnoliales syncarpiques.

En effet, chez les Canellaceae, où la syncarpie est de règle (Wilson, 1966), la soudure des deux à six carpelles engendre également un gynécée uniloculaire à placentation pariétale. Mais à la différence des Annonaceae, Leinfellner (1967b) observe dans le genre africain *Warburgia* que le gynécée n'est fertile que dans sa partie supérieure. En effet, chaque carpelle individuel a une zone basale ascidiée, de sorte que le gynécée est pluriloculaire à la base et sans ovules à ce niveau. Les ovules sont insérés sur deux rangées, par

zone de soudure carpellaire dans la partie supérieure uniloculaire.

Dans le genre *Takhtajania*, seule Winteraceae à ovaire syncarpe uniloculaire (Leroy, 1977, 1978), l'ovaire est constitué par la soudure de deux carpelles comparables aux carpelles libres des autres Winteraceae (Vink, 1978), dont la base est ascidiée, alors qu'elle ne l'est apparemment pas dans le genre *Takhtajania*.

Outre la réduction du nombre de carpelles, l'évolution de la structure carpellaire des Magnoliales se manifeste donc par deux tendances majeures: 1) la perte de l'ascidiation et 2) l'acquisition de la syncarpie. En Afrique, ce sont encore les Annonaceae qui montrent la plus grande diversification carpellaire, puisqu'on y retrouve ces deux tendances évolutives avec, en outre, très rarement, des résidus d'ascidiation dans les carpelles libres (*Anaxagorea*). Les Myristicaceae et les Annonaceae restent cependant très étroitement liées par leurs carpelles libres non ascidiés, à base unifaciale, tandis que le carpelle syncarpe des Canellaceae, représentant une étape fonctionnelle importante, établit le lien avec les Annonaceae. Si les Winteraceae présentent une structure carpellaire souvent très ascidiée, leur conférant un caractère particulièrement primitif, on constate cependant qu'il existe dans cette famille une tendance à la syncarpie (*Zygogynum*) parfaitement réalisée dans le genre *Takhtajania* qui semble, par ailleurs, avoir perdu toute trace d'ascidiation, comme dans le genre *Tasmannia* (Ehrendorfer et al., 1979).

Implications Evolutives

L'étude comparative des structures reproductives (pollen-carpelle) des Magnoliales africaines témoigne d'une vaste diversification dans laquelle l'unité des Annonaceae, Myristicaceae, et Canellaceae peut être clairement reconnue, mais qui paraît isoler le genre *Takhtajania* et les Winteraceae. Elle montre, d'autre part, que la présence de types plus évolués, comme il en existe en particulier dans les Annonaceae, n'exclut pas nécessairement les formes aussi primitives que dans les autres groupes dont elles sont affines. La diversification en mosaïque des formes actuelles de Magnoliales indique seulement des tendances évolutives dont l'enchevêtrement ne peut que nous convaincre de prudence et de modestie dans toute hypothèse avancée sur l'origine des angiospermes.

En revanche, chaque découverte paléobotanique apporte la preuve de l'existence ancienne du caractère supposé primitif chez les plantes actuelles et permet d'argumenter plus solidement les différentes théories fondées sur les affinitiés systématiques et morphologiques. Dans ce domaine, de grands progrès ont été faits depuis une quinzaine d'années.

Le spectre palynologique du Crétacé inférieur (Doyle, 1969, 1977, 1978; Doyle et al., 1975, 1979, 1982; Doyle & Hickey, 1976; Walker et al., 1983; Walker & Walker, 1984) montre l'extrême diversification des types polliniques (Muller, 1970) et confirme la diversité des types monosulqués angiospermiens les plus anciens. De nombreux auteurs ont souligné la ressemblance de certains de ces types polliniques monosulqués, réticulés, columellaires les plus anciens (*Clavatipollenites*) avec des groupes de Magnoliales actuelles: Chloranthaceae, Canellaceae, Myristicaceae, conduisant même certains à voir dans le pollen des Chloranthaceae le type originel des angiospermes. Cependant, les corrélations établies dans l'étude comparative des Magnoliales actuelles conduit plutôt à interpréter le type sulqué, non columellaire, tel que celui des Degeneriaceae et certaines Annonaceae, comme le plus primitif (Walker, 1976; Le Thomas, 1981). Pourtant, aucun pollen comparable n'a encore été découvert parmi les fossiles du Crétacé inférieur, pour des raisons faciles à imaginer et que Walker & Walker (1984) ont fort bien résumeés fragilité de l'exine entraînant une mauvaise fossilisation, trop faible pourcentage dans les sédiments, confusion possible avec les pollens sulqués des gymnospermes. On ne peut évidemment exclure l'opportunité d'une telle découverte paléobotanique pour appuyer l'hypothèse que les Magnoliales constituent l'ordre central le plus primitif des Magnoliidae (Walker & Walker 1984), mais il peut paraître actuellement prématuré de l'affirmer.

En revanche, une intéressante série morphologique a été décrite dans le genre *Afropollis* (Doyle et al., 1982), découvert dans l'Aptien inférieur de la province Nord-Gondwanienne africaine. Il révèle en effet une grande diversité des apertures comme de la structure de l'exine. Jusqu'au Cénomanien il se diversifie avec des formes operculées, zonasulculées, inaperturées hétéropolaires et isopolaires, une exine semitectée, lâchement réticulée, pouvant être columellaire ou non. Dans ce cas, les corrélations établies entre les différents caractères polliniques conduisent les auteurs à considérer que la condition hété-

ropolaire operculée de *Afropollis operculatus* ne peut être que dérivée du type commun monosulquée hétéropolaire, réticulé; ainsi, dans cette même espèce, ils concluent également au caractère primitif de la columelle, puisqu'elle y est associée au même type d'ornementation réticulée que dans la grande majorité des pollens des premières angiospermes. Cette série crétacéenne rappelle quelque peu la série qui est décrite ci-dessus dans les Annonaceae, et dans laquelle l'hétéropolarité du type sulqué de base est conservée dans le type operculé (columellaire-réticulée) dérivé, tandis qu'elle disparaît dans le type équatoriosulqué dont la couche infratectale de l'exine est grenue et l'ornementation verruqueuse. Les deux types de pollens sulqués, columellaires ou non, étant présents dans les Annonaceae, il est donc, dans ce cas, plus délicat de déduire que la columelle est primitive, d'autant que les formes isopolaires peuvent être columellaires ou grenues et que les différentes corrélations tenderaient à montrer l'inverse.

Les rapides progrès de la palynologie du Crétacé ne sont donc pas encore suffisants pour éclaircir totalement le mystère de l'origine des angiospermes, mais ils contribuent de façon très réelle à montrer que, si les Magnoliales ne représentent pas nécessairement l'archétype des angiospermes, elles ont conservé un plus grand nombre de caractères polliniques primitifs que d'autres dicotylédones actuelles (Hickey & Doyle, 1977; Le Thomas, 1981). La découverte de nouvelles séries fossiles devraient permettre d'interpréter avec plus de certitude celles qui peuvent être décrites dans les groupes actuels.

Jusqu'à ces dernières années, les études palynologiques et foliaires (Wolfe, 1972; Wolfe et al., 1975; Hickey & Doyle, 1977) ont été prédominantes dans les recherches sur les premières angiospermes; plus récemment, les données paléobotaniques sur les structures florales (Dilcher, 1979; Retallack & Dilcher, 1981; Dilcher & Crane, 1984; Crane & Dilcher, 1984) ont apporté des éléments fort intéressants dans la connaissance des premières angiospermes, susceptibles de faire progresser les hypothèses phylogéniques des plantes à fleurs. En particulier, la découverte par Dilcher (1979) dans le Crétacé moyen, de petites fleurs unisexuées, groupées en chatons et associées à des masses de pollens monosulqués, semblables à celles de *Retimonocolpites* (Doyle et al., 1975), a-t-elle pu quelque peu dérouter les défenseurs de l'unique théorie Magnolidienne, et satisfaire ses détracteurs. Comme le soulignait cependant très justement Dilcher, ces nouvelles données fossiles indiquaient seulement la diversité déjà très grande des structures reproductives, comparable à celle des pollens et des feuilles, et leur rapide diversification dès le début du Crétacé. Ces conclusions ont d'ailleurs été confirmées par les structures florales (*Archaeanthus*) et fructifères (*Lesqueria*) du Crétacé moyen qu'il a récemment décrites avec Crane & Dilcher (1984) en les rapprochant étroitement des Magnoliales, sans pour cela pouvoir les rattacher directement à un groupe actuel.

Ainsi, les paléobotanistes eux-mêmes, restent-ils donc encore très réservés sur la phylogénie des angiospermes primitives, et avec juste raison semble-t-il. Ils apportent cependant la preuve que de nombreux fossiles du Crétacé (pollen, feuilles, fleurs, fruits) appartiennent avec certitude au type Magnolien, et confirment ainsi l'ancienneté des Magnoliales, dont l'extinction aurait pu commencer dès cette époque, ce qui expliquerait la difficulté d'interpréter des séries actuelles souvent très incomplètes. Ils soulignent aussi l'extrême diversification des angiospermes à cette période, excluant, dans l'état actuel des connaissances, toute hypothèse formelle sur l'origine des angiospermes et leur archétype qu'il convient peut-être de rechercher à une époque antérieure.

Quoiqu'il en soit, les données paléobotaniques ne contredisent nullement l'unité des Magnoliales africaines, soulignées par l'étude comparative des structures reproductives actuelles qui semblent indiquer que ce groupe d'angiospermes aurait eu une origine commune Gondwanienne (Raven & Axelrod, 1974; Wolfe, 1981). Les tendances évolutives du pollen paraissent, pour le moment, mettre en évidence un plus grand nombre de types primitifs en Afrique (Le Thomas, 1981, 1984) et témoigner de l'ensemble des potentialités qui ont pu se différencier parallèlement ou indépendamment sur chaque continent après la dérive des continents africain et américain.

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DISTRIBUTION AND EVOLUTION OF THE MADAGASCAR BIGNONIACEAE[1]

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ABSTRACT

Madagascar is the world's second greatest center of diversity for Bignoniaceae, exceeded only by the much larger neotropical region. There are representatives of two tribes on Madagascar. Three of the four genera of the wind-dispersed tribe Tecomeae are shared with continental Africa (two of them also with tropical Asia), and the fourth Tecomeae genus is not very distinct from shared *Fernandoa*. The Madagascar Tecomeae are concentrated in the drier western half of the island and most of them are widespread. Most of the Madagascar Bignoniaceae belong to the near-endemic mammal-dispersed tribe Coleeae; the only extra-Madagascan species of this tribe is *Kigelia* on continental Africa. The Coleeae, probably mostly dispersed by lemurs, have radiated into five distinct genera and 50 species on Madagascar, including three species in the Comores, one on Mauritius, and one on the Seychelles. The Coleeae are concentrated in the moist forests of the eastern side of the island and have many locally endemic species especially in the northern part of Madagascar. A number of lines of evidence suggest that much of the generic radiation of the Madagascar Bignoniaceae may have preceded the definitive breakup of Gondwanaland.

RÉSUMÉ

Madagascar est le deuxième plus grand centre de diversité au monde pour les Bignoniacées, la première place allant seulement à la bien plus vaste région néotropicale. Deux tribus sont représentées à Madagascar. Trois des quatre genres des Tecomeae, qui sont dispersés par le vent, se trouvent également en afrique continentale (deux d'entre eux sont aussi en asie tropicale), et le quatrième genre n'est pas très distinct de *Fernandoa*. Les Tecomeae de Madagascar sont localisées surtout dans la moité occidentale plus aride de l'île et la plupart d'entre elles sont dispersées par le vent. La majorité des Bignoniacées de Madagascar appartiennent à la tribu des Coleeae, presqu'endémique et dispersée par les mammifères; la seule espèce de cette tribu hors de Madagascar est le *Kigelia* en afrique continentale. Les Coleeae, qui sont probablement surtout dispersées par des lemurs, se sont diversifiées en cinq genres distincts et 50 espèces à Madagascar, y compris trois espèces aux Comores, une sur l'Ile Maurice, et une aux Seychelles. Les Coleeae se trouvent principalement dans les forêts humides dans la partie est de l'île et ont de nombreuses espèces locales endémiques, surtout dans la partie nord de Madagascar. Plusieurs types de données permettent de suggérer qu'une bonne partie de la diversité générique des Bignoniacées malgaches a pu précéder la séparation définitive de Gondwanaland.

Madagascar is the world's second greatest center of diversity for Bignoniaceae, exceeded only by the much larger neotropical region. There are 65 species of Bignoniaceae on Madagascar, over twice as many as on continental Africa (32 spp.), the Australian region (24 spp., including the Sahul shelf islands and New Caledonia), or temperate Asia (26 spp.), and many more than in tropical/subtropical Asia (50 spp.) as well. This paper examines the distributional and putative evolutionary patterns of the Madagascar Bignoniaceae in an attempt to determine why there are so many species of Bignoniaceae on Madagascar.

At first glance, Bignoniaceae, a member of the highly advanced sympetalous Asteridae, would not seem a likely candidate for a family with unusually strong representation on Madagascar. Madagascar is much better known for its primitive relict taxa. Some of these, like *Takhtajania perrieri* Winteraceae (Leroy, 1977) and *Ascarinopsis coursii* Chloranthaceae (Humbert & Capuron, 1955) are veritable living fossils, each constituting a monotypic, endemic genus restricted to a single massif, and each the only African-area representative of a family generally considered among the most primitive of all flowering plants. Not coincidentally, vesselless Winteraceae, considered by many botanists to come nearer to the hypothetical ancestral angiosperm prototype than any other family (Cronquist, 1981), and Chloranthaceae, with a male inflorescence sometimes suggested to be homologous to a single strobiluslike preflower (Burger, 1977;

[1] I thank the National Geographic Society for support of my fieldwork in Madagascar, and the National Science Foundation for supporting my studies of Bignoniaceae.

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Leroy, 1983) and similar to recently discovered mid-Cretaceous fossils (Dilcher, 1979), are the only two extant angiosperm families known to have a Lower Cretaceous fossil record (Coetzee & Muller, 1984). Such taxa, botanical equivalents of the tenrecs (which are similar to the most primitive eutherian mammals), are typical of the archaic organisms commonly associated with Madagascar. Winteraceae and Chloranthaceae are both widespread in the fossil record, were present in Africa at least until the Miocene (Coetzee & Muller, 1984), and have obviously survived, albeit barely, on Madagascar due to the protection provided by its island situation.

Moreover, not all these archaic taxa are at evolutionary dead ends. Only slightly less primitive are families like Monimiaceae, sometimes cited as the botanical equivalent of the lemurs, which has radiated into six genera, all endemic, and 50 species in the Malagasy region (Lorence, 1985); diversification in floral morphology in this group is so great that it has been claimed to span a similar range as the shift from gymnospermy to angiospermy (Endress & Lorence, 1983). Monimiaceae are widespread in the Gondwanan continents, including a subfamily on Ceylon, another disjunct between West Africa and South America, a third disjunct between the Mascarenes and Chile, and a fourth strongly austral from Australasia to Chile, as well as a more widely distributed group with the Malagasy concentration. An archaic assemblage of Thealean taxa, including the two Madagascar endemic families Sarcolaenaceae (10 genera, 35 species) and Sphaerosepalaceae (2 genera, 18 species), represents a similar evolutionary level to Monimiaceae: very ancient groups which have nevertheless proliferated extensively on Madagascar. Interestingly the unmistakable pollen tetrads of *Xylolaena* of the Sarcolaenaceae have recently been discovered in the Miocene of the South African Cape region (Coetzee & Muller, 1984). It is highly probable that the Madagascar representatives of such archaic taxa are generally derived from more widespread ancestral stocks that reached Madagascar more or less directly from Africa before the breakup of Gondwanaland (cf. Raven & Axelrod, 1974; Axelrod & Raven, 1978).

At the other extreme are groups that, despite having evolved endemic taxa on Madagascar, are certain to have reached Madagascar rather recently by long-distance dispersal (e.g., *Helichrysum, Senecio*) or possibly even human introduction (*Pavonia, Sida, Cyperus*) (Koechlin, 1972). *Rhipsalis* is a good example, with *R. baccifera,* the most widespread neotropical species of cactus, having reached the paleotropics by long-distance dispersal, where it occurs in Africa, Ceylon, and Madagascar and has given rise on the latter to two derivative species (Barthlott, 1983).

In a recent summary of Madagascar floristics Leroy (1978), following Raven & Axelrod (1974), emphasized that, with acceptance of the theory of plate tectonics, the much debated dichotomy of long-distance dispersal vs. overland migration becomes less critical. Madagascar probably effectively separated from the African mainland about 100 million years ago (Raven & Axelrod, 1974). Apparently Madagascar started to separate from the mainland much earlier, perhaps beginning in mid-Jurassic, but at first mostly sliding south along the African coast (Rabinowitz et al., 1983). Effective separation from the continental margin of Kenya and Somalia occurred by at least 95 million years ago but there may have been additional connections via intermediate islands (Raven & Axelrod, 1974; Axelrod & Raven, 1978; Coetzee & Muller, 1984). Thus many older angiosperm families were undoubtedly on Madagascar when it definitively separated from the African mainland, with more recently evolved families no doubt reaching it subsequently over relatively minor sea gaps until rather late in the Cretaceous.

The youngest angiosperm families, like Compositae, which is well represented on Madagascar and is in fact the largest family in the flora (Leroy, 1978), must have reached Madagascar over considerable water gaps, a not unlikely scenario in view of the prevalence of this family on oceanic islands like Hawaii and the Galapagos, but contrary to earlier authors like Humbert (1959) who thought that essentially all speciation on Madagascar must have represented differentiation from the ancestral flora.

The above review sets the stage for the question to be addressed here. How do Bignoniaceae fit into this scenario? The degree of evolutionary advancement of the family might suggest that it would be an unlikely candidate for arrival via direct overland migration in mid-Cretaceous times. This "johnny-come-lately" theory would also be supported by the observation that there are few generic similarities between the Bignoniaceae of continental Africa and the Neotropics, contrary to the situation in many phylogenetically less-advanced groups (e.g., Gentry, 1982).

On the other hand, most Bignoniaceae are poor candidates for overwater dispersal, since their mammal-dispersed and pterochorous seeds are not effective for very long-distance dispersal (Gentry, 1983a; see also Carlquist, 1974).

An overview of Bignoniaceae taxonomy and phytogeographic patterns provides relevant background information. Worldwide, the family includes over 800 species, divided into eight tribes (Gentry, 1980). A preponderance (645, or 77%) of the species and two major tribes—Crescentieae, with indehiscent fruits and mostly mammal-dispersed seeds, and Bignonieae, tendrillate lianas with fruits dehiscing parallel to the septum—are exclusively neotropical. There are also three additional small neotropical tribes. Another small tribe, Oroxyleae, is confined to Southeast Asia. Tribe Coleeae, traditionally treated as part of Crescentieae, with which it shares indehiscent fruits, but clearly derived from a different Tecomeae ancestral plexus, is endemic to Madagascar and adjacent islands except for ditypic *Kigelia* on the African continent. The final tribe, Tecomeae, by far the most widespread, is pantropical and even includes some temperate zone species. Nearly all the species have wind-dispersed seeds with capsules dehiscing perpendicular to the septum. Except for *Kigelia,* this is the only tribe represented on continental Africa. Half of the Madagascar genera, but relatively few species, belong to Tecomeae.

On the basis of chromosome number and the retention in several species of such presumed primitive morphological features as five fertile stamens, Oroxyleae are probably close to the basal stock of the family (Goldblatt & Gentry, 1979). Tecomeae is also probably close to the ancestral plexus of the family and it is likely that other tribes—including Bignonieae in South America, Crescentieae in Central America, and Coleeae in Madagascar—are directly derived from Tecomeae (Gentry, 1974, 1976). Only Tecomeae and Coleeae are relevant to this paper.

Table 1 lists the genera of Madagascar Bignoniaceae. Three of the four genera of Tecomeae are shared with continental Africa, *Rhigozum* uniquely so, and *Fernandoa* and *Stereospermum* also with tropical Asia. *Rhigozum,* interesting because of its retention of the primitive 5-staminate condition and for its cross-African disjunction from the southwest to the northeast, has seven species on the continent and one in similarly dry habitats on Madagascar. *Stereospermum,* reversing the species concentration, has ten species on Madagascar but only half that number in Africa; in addition, there are four tropical Asian species. *Stereospermum* is taxonomically very distinctive on account of the swollen septum with depressions in which the seed bodies are immersed. There has been much taxonomic confusion surrounding the delimitation of the third genus, *Fernandoa.* The three Madagascar *Fernandoa* species were formerly segregated as *Kigelianthe,* more by biopolitical accident than for taxonomic reasons (Gentry, 1975). Van Steenis (1976) suggested that the tropical Asian genera *Spathodeopsis, Haplophragma,* and *Hexaneurocarpum,* plus an errant species of *Radermachera* (*R. bracteata* P. Dop), are congeneric with *Fernandoa.* At least in the case of monotypic *Spathodeopsis* this is surely correct, but *Haplophragma* (with which *Hexaneurocarpum* is synonymous) seems to me to be better maintained as distinct. On the other hand, rare and monotypic *Lamiodendron* of New Guinea might well be a second Australasian species of *Fernandoa.* As I delimit it, *Fernandoa* is distinctive especially in its broadly campanulate red to yellow bird-pollinated flowers with a nonspathaceous calyx. The fourth Madagascar genus of Tecomeae is monotypic *Perichlaena,* very similar to *Fernandoa* from which it differs in its liana habit and narrower, more zygomorphic flowers. *Perichlaena* was clearly derived from *Fernandoa* and could be accommodated in that genus with only minor stretching of the generic limits.

Thus the four Madagascar Tecomeae genera represent at least three different introductions from (or common stocks independently shared with) the African continent. In one of these (*Rhigozum*) the Madagascar taxon merely diverged

TABLE 1. Genera of Malagasy Bignoniaceae.

Tecomeae
Fernandoa (3 spp.)
Perichlaena (1 sp.)
Rhigozum (1 sp.)
Stereospermum (10 spp.)
Coleeae
Colea (21 spp., including 1 on Mauritius and 1 in Seychelles)
Ophiocolea (5 spp., including 1 in Comores)
Phyllarthron (15 spp., including 1 in Comores)
Phylloctenium (2 spp.)
Rhodocolea (7 spp.)

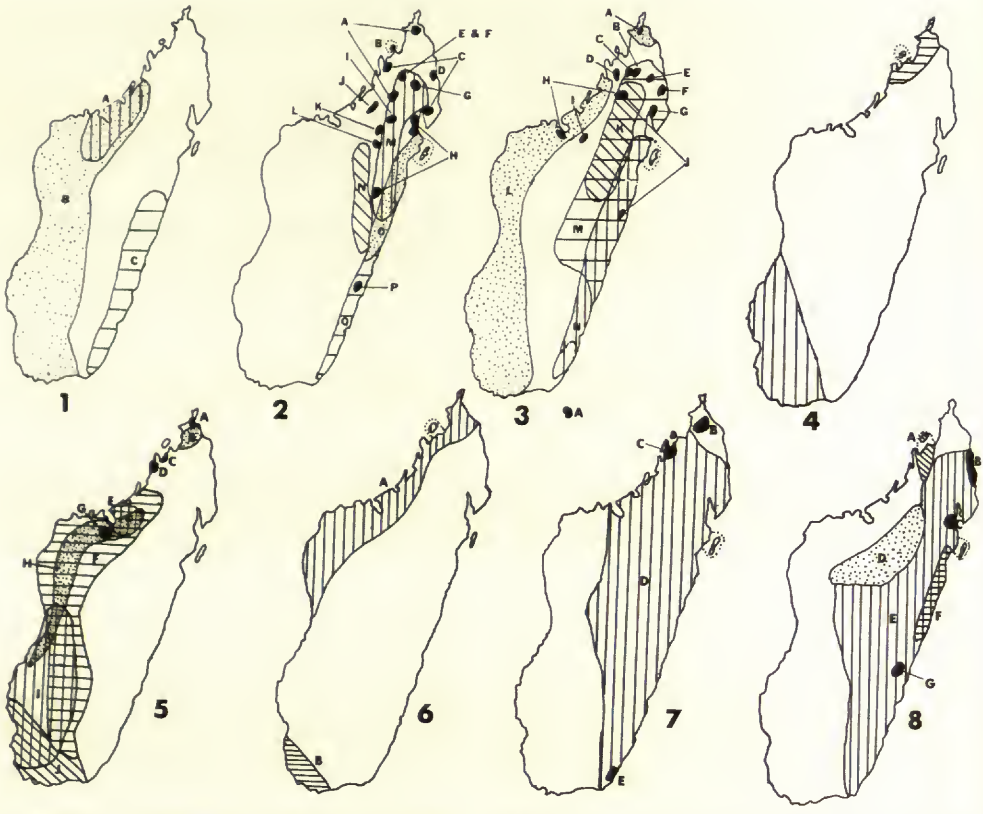

FIGURE 1. Distribution of Madagascar Bignoniaceae. Maps 1–3 from Gentry, 1983b; Maps 4–7 original, in large part after Perrier, 1938a with additional data from Capuron, 1960, 1970, and Gentry, 1977 and unpublished. MAP 1: *Fernandoa.*—A. *F. macrantha* (Baker) A. Gentry.—B. *F. madagascariensis* (Baker) A. Gentry.—C. *F. coccinea* (Scott Elliot) A. Gentry. MAP 2: *Colea.*—A. *C. barbatula* Perrier.—B. *C. purpurascens* Seemann.—C. *C. hirsuta* DC.—D. *C. asperrima* Perrier.—E. *C. rubra* Perrier.—F. *C. alba* Perrier.—G. *C. myriaptera* Perrier.—H. *C. nana* Perrier.—I. *C. campenoni* Perrier.—J. *C. muricata* Perrier.—K. *C. lutescens* Perrier.—L. *C. concinna* Baker.—M. *C. fusca* Perrier.—N. *C. lantziana* Baillon.—O. *C. tetragona* DC.—P. *C. alata* Perrier.—Q. *C. obtusifolia* DC. Not shown are *C. seychellarum* Seemann in the Seychelles and *C. colei* Perrier on Mauritius. MAP 3: *Phyllarthron.*—A. *P. suarezense* Perrier.—B. *P. bilabiatum* A. Gentry.—C. *P. laxinervium* Perrier.—D. *P. megaphyllum* Capuron.—E. *P. multiflorum* Perrier.—F. *P. cauliflorum* Capuron.—G. *P. antongiliense* Capuron.—H. *P. megapterum* Perrier.—I. *P. subumbellatum* Perrier.—J. *P. articulatum* (Desf.) K. Schum.—K. *P. humblotianum* Perrier.—L. *P. bernieranum* Seemann.—M. *P. madagascariense* (Bojer) K. Schum.—N. *P. ilicifolium* Perrier. Not shown is *P. comorense* (Bojer) DC. *Paraphyllarthron* (Leroy, 1972) is included in *Phyllarthron.* MAP 4: *Perichlaena* and *Rhigozum.*—Top. *P. richardii* Baillon.—Bottom. *R. madagascariense* Drake. MAP 5: *Stereospermum.*—A. *S. boivinii* (Baillon) Perrier.—B. *S. longiflorum* Capuron.—C. *S. rhoifolium* (Baillon) Perrier.—D. *S. hildebrandtii* (Baillon) Perrier.—E. *S. arcuatum* Perrier.—F. *S. euphorioides* (Bojer) DC.—G. *S. tomentosum* Perrier.—H. *S. undatum* Perrier.—I. *S. variabile* Perrier.—J. *S. nematocarpum* (Bojer) DC. MAP 6: *Phyllocteniu*m.—A. *P. bernieri* Baillon.—B. *P. decarianum* Perrier. MAP 7: *Ophiocolea.*—A. *O. comorensis* Perrier.—B. *O. veleutina* Perrier.—C. *O. decaryi* Perrier.—D. *O. floribunda* (Bojer) Perrier.—E. *O. delphinensis* Perrier. MAP 8: *Rhodocolea.*—A. *R. boivinii* (Baillon) Perrier.—B. *R. perrieri* Capuron.—C. *R. nobilis* Baillon.—D. *R. telfairiae* (Bojer) Perrier.—E. *R. racemosa* (Lam.) Perrier.—F. *R. involucrata* (Bojer) Perrier.—G. *R. linearis* Perrier.

enough to become specifically distinct, in another (*Stereospermum*) it radiated into a number of species differentiated largely on vegetative grounds, and in the third (*Fernandoa*) it diverged to the extent that one of the derivatives is more or less generically distinct. These wind-dispersed genera are best represented in the dry parts of Madagascar with most of their species fairly wide-

ranging and largely allopatric (Fig. 1). If only the Tecomeae were considered, Madagascar's Bignoniaceae representation would be unexceptional, with less than half as many species as continental Africa. Since several lines of evidence suggest that Tecomeae may be old enough to date back well into the Cretaceous (Gentry, 1987), it is probable that these genera, along with the pinnate-leaved neotropical genera *Tecoma* and *Campsidium,* were a part of the old West Gondwanan flora shared by Africa and Madagascar before the latter's definitive separation from the mainland.

However, this scenario presents a curious enigma. Unlike the situation in many other groups, the South American Tecomeae, with two exceptions, are not closely related to paleotropical genera. Only basically Andean *Tecoma* seems close to an African genus, South African *Tecomaria.* Chilean *Campsidium* also has Old World affinities, but whether it is closer to North Temperate *Campsis,* disjunct between eastern North America and eastern Asia, or to primarily Australian *Tecomanthe* remains conjectural. In neither case are there shared genera or even closely related genera in Madagascar and South America. Since much evidence, biogeographical as well as geological, indicates that Madagascar separated earlier from Africa than did South America (e.g., Raven & Axelrod, 1974; McKenna, 1981), it seems curious that none of the presumably old genera shared between Madagascar and Africa are in South America. With the exception of *Tecoma-Tecomaria,* the differentiation of Tecomeae on opposite sides of the Atlantic would appear on phytogeographical grounds to have succeeded Gondwana breakup, whereas that on opposite sides of the Mozambique Channel preceded it. Such a pattern would only make sense if the ancient geological separation of Madagascar were decoupled from the much more recent biological separation. Since new geological (Rabinowitz et al., 1983) and palynological (Herngreen & Chlonova, 1981; Herngreen et al., 1982; Coetzee & Muller, 1984) evidence is compatible with a relatively direct and relatively southern late connection, such a decoupling of geological and biological separation seems plausible.

The Coleeae are much more interesting than the Tecomeae in Madagascar. Traditionally this group has been classified with the otherwise predominantly Central American tribe Crescentieae, which has a similarly indehiscent fruit. Based on this taxonomy, Leroy (1978) concluded that Crescentieae represent an old West Gondwanan lineage. However, it now seems clear that the indehiscent-fruited neotropical genera represent convergent evolution with the indehiscent-fruited Madagascar taxa, the two groups being derived from different Tecomeae stock (Gentry, 1974, 1976, 1980). Thus the Coleeae on Madagascar would appear to represent a unique and autochthonous evolutionary switch from wind dispersal to mammal dispersal.

The existence of *Kigelia* on continental Africa confounds this picture. *Kigelia* shares the pinnately compound leaves that characterize Coleeae, rather than the palmately compound ones (or their simple-leaved derivatives) that characterize the Crescentieae, and almost certainly shares an indehiscent-fruited common ancestor with Coleeae. This would suggest that evolution of the indehiscent fruit of Coleeae probably occurred before the total isolation of Madagascar. *Kigelia* is largely baboon-dispersed (Lieberman et al., 1979) and the Coleeae presumably lemur-dispersed. Thus the original differentiation of indehiscent-fruited Bignoniaceae in the Afro-Malagasy region may well have paralleled the early radiation of lemuriforms. It is now generally accepted that the Madagascar lemurs of today represent several different independent introductions from the continent rather than radiating from a single introduction (Tattersall, 1982). Quite probably some of the generic differentiation of Colleae took place on the African continent as well. Subsequently the plants, like the lemurs, underwent extensive radiation in Madagascar but barely managed to survive in the more hostile conditions created by climatic deterioriation and newly evolving competitors on continental Africa.

Ultimately it matters little that the Coleeae arose prior to the definitive separation of Madagascar from Africa. The major radiation of lemur-dispersed Coleeae in Madagascar, whose end products we see today, is a beautiful example of evolutionary diversification, and it is thanks to this diversification that there are so many Madagascan species of Bignoniaceae.

Elsewhere, I have described probable major evolutionary trends and relationships within the Madagascar Coleeae (Gentry, 1976) as well as some of the phytogeographical consequences of their dispersal ecology (Gentry, 1983b). Here I would like to weave these two threads together into an overview of the pattern of distribution and evolution of tribe Coleeae.

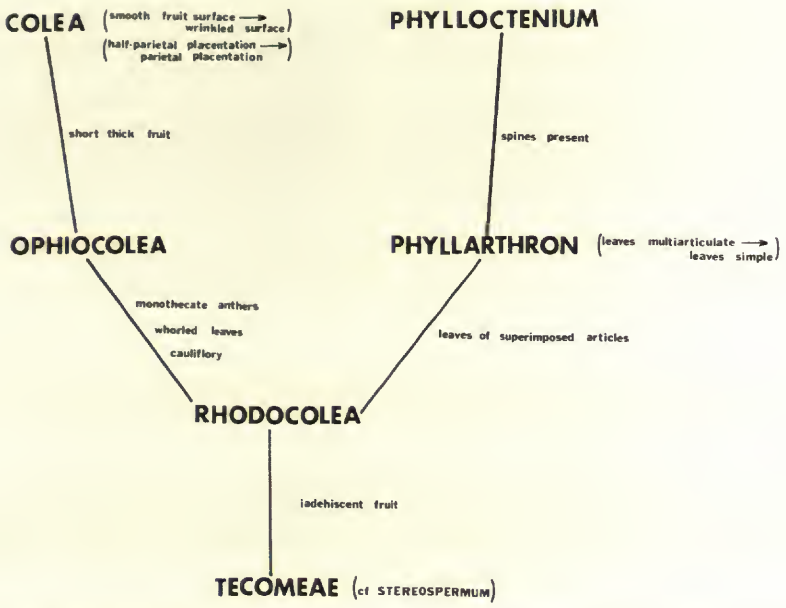

FIGURE 2. Evolutionary trends in Madagascar Coleeae. Note basal position of *Rhodocolea,* which differs from Stereospermum (Tecomeae) only in its indehiscent fruit. The definitive characteristic(s) of each genus is indicated along line of descent below it; major changes within genera are indicated by parentheses, and the advanced character state is present in derivative genera. From Gentry, 1976.

The critical nonmissing link between the Coleeae and Tecomeae is *Rhodocolea. Rhodocolea* has all of the putatively primitive character states of the tribe. In fact the only real difference between *Rhodocolea* and *Stereospermum* is the former's indehiscent fruit. Figure 2 (from Gentry, 1976) summarizes the evolutionary steps that have given rise to the five Madagascar Coleeae genera. One evolutionary line leading to *Ophiocolea* and *Colea* has featured changes in flowers and fruits. Both *Ophiocolea* and *Colea* differ from the rest of the Coleeae in monothecate anthers, cauliflory, and the presence of whorled rather than opposite leaves. *Ophiocolea* has a similar long narrow fruit to that of *Rhodocolea,* but in *Colea* the fruit is short and thick. Placentation is fully axile in *Ophiocolea* and *Rhodocolea* but half parietal to parietal in more highly advanced *Colea.*

The second main evolutionary line in Coleeae features vegetative specialization. In *Phyllarthron* the leaflets of *Rhodocolea* are suppressed and the rachis expanded so that the compound leaves of the latter are converted into a unique series of segmented articles equivalent to the winged rachis of the ancestral pinnately compound leaf. Within *Phyllarthron* there is a general trend toward both increasing width in and loss of the articles so that in the extreme case, *P. ilicifolium* Perrier, formerly segregated as the genus *Zaa,* the leaf consists of merely the basal article and is effectively simple. *Phylloctenium* is closely related to the simple-leaved species of *Phyllarthron* but differs from them in such xeric adaptations as the presence of spines and in a somewhat rachitic, dichotomously-branched, shrubby habit with smaller leaves.

Figure 3 (from Koechlin, 1972) is an overview of the major phytogeographic regions of Madagascar. In general the center of the island is a rather cool plateau, often ca. 1,000 m in altitude, with a few isolated mountains in excess of 2,000 m rising from it. The western coastal lowlands are (or were) covered by dry forest, and the eastern coastal lowlands by tropical moist forest. The north tip of the island is dry forest, isolated from the rest of the dry forest by a phytogeographically distinct patch of wet forest that makes up the Sambirano region on the west coast, ashore from Nosy Bé. Finally, there is a unique dry thorn scrub vegetation dominated by Didiereaceae and succulent Euphorbiaceae in the extreme southwest.

Phytogeographically and ecologically, the

FIGURE 3. Phytogeographic regions of Madagascar (from Koechlin, 1972, after Humbert).—1. East area, moist forest.—2. Sambirano region, moist forest.—3 and 4. Center area, eastern and western slopes, respectively.—5. High mountains.—6. West area, dry forest.—7. Southwest area, thorn scrub.

mammal-dispersed genera of Madagascan Bignoniaceae differ from the wind-dispersed Tecomeae of Madagascar in several important ways. Wind-dispersed Tecomeae (Fig. 1) are concentrated in the dry forests of the western half of the island. Only one fairly widespread Tecomeae species, *Fernandoa coccinea* (Scott Elliot) A. Gentry, and two locally endemic *Stereospermum* species of the Sambirano region occur in the moist forest at all. The complete absence of wind-dispersed Bignoniaceae from most of the wetter half of the island is striking. The wind-dispersed species show little local endemism. Altogether there are only five locally endemic Tecomeae species—four species of *Stereospermum* near the island's north tip and an additional one south of Majunga. The greatest diversity of Tecomeae is in the Majunga-Ankarafantsika region where up to seven Tecomeae species can occur in the same 1° grid square. However, Tecomeae are well represented even in the extremely dry southwestern Didiereaceae forests to which two species, *Rhi-*

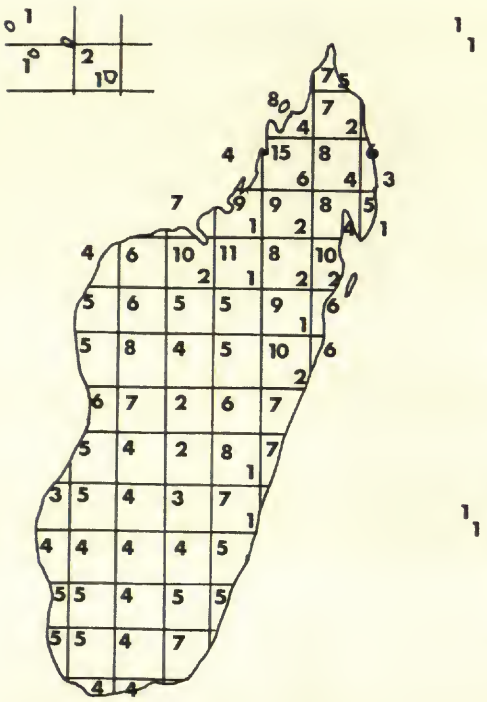

FIGURE 4. Distribution of diversity and endemism in Malagasy Bignoniaceae species by degree grid squares. Number at top left of each square is total number of species in that grid square. Number at lower right of each square is number of locally endemic species in that square. Several species with two isolated collection stations are counted as locally endemic at both sites. Data from Figure 1.

gozum madagascariensis and *Stereospermum nematocarpon,* are almost restricted and in which two more widespread species also occur.

The mammal-dispersed Coleeae are almost the mirror image of the Tecomeae in several respects. They are concentrated in exactly those wet forests of the eastern half of Madagascar where Tecomeae are so conspicuously absent. Up to 10 or 11 species of Coleeae co-occur in several different degree grid squares. Except for secondarily xeric-adapted *Phylloctenium,* the only real dry area Coleeae is *Phyllarthron bernierianum* Seem. In the dry forest as a whole there are only two widespread species with mammal-dispersed fruit, *Phyllarthron bernierianum* and *Phylloctenium bernieri* Baillon, both morphologically highly specialized for xeric conditions. In addition, there is a second, even more xeric-adapted species of *Phylloctenium* in the southwestern Didiereaceae forest. Several, perhaps all, of the locally endemic species of *Colea* and *Phyllarthron* in the far north and in the Majunga region are actually restricted to mesic forest patches along streams in protected canyons, e.g., *Phyllarthron megapterum* Perrier (*Gentry 11509, 11763*) and *P. suarezense* Perrier (Perrier, 1938a, 1938b).

Also very unlike the Tecomeae, Coleeae are highly prone to local endemism. High local endemism tends to be generally concomitant with mammal dispersal (Gentry, 1983b). The same pattern of high local endemism is shown by the neotropical Crescentieae, in strong contrast to the widespread distributions typical of wind-dispersed neotropical Bignoniaceae. Presumably the relatively localized seed dispersal provided by nonflying mammals leads to sufficient reduction in dispersal-mediated gene flow to promote local speciation.

Figure 4 compares local endemism by degree grid squares with data from the distribution maps of Figure 1. All of the locally endemic Bignoniaceae except the few *Stereospermum* species noted above belong to Coleeae—4 *Ophiocolea* species (including the one on Mayotte), 4 *Rhodocolea* species, 10 species of *Phyllarthron,* and 13 of *Colea* (plus one species each on Mauritius and in the Seychelles). Almost all of these endemics are concentrated in the north end of the island (Figs. 1, 4). Except for a few endemics around Diego Suarez, all of these locally distributed species are found in wet or moist forests. The grid square that includes Tsaratanana, the highest mountain of Madagascar, has no fewer than five locally endemic species of Coleeae (plusan endemic *Stereospermum*).

The endemic species of Coleeae are not noticeably concentrated in coincident centers of endemism. Instead each seems to represent a unique case of speciation in a particular local habitat. Except for xeric-adapted *Phylloctenium,* the various Coleeae genera show extremely similar distributional patterns, likely reflecting a common evolutionary history. Each genus has one or two species widespread in the eastern moist forests and several to many localized endemics, in some cases [e.g., *Phyllarthron bilabiatum* A. Gentry (Gentry, 1977)] almost certainly derived from one of the widespread taxa. Each genus has at least one endemic species haphazardly scattered in the central or southern part of the east coast forest. Each genus except *Rhodocolea* has one or two outlying species on adjacent island groups—Comores, Seychelles, Mascarenes—that

are now considered fragments tracing from the Gondwanan breakup.

Doubtless, early Coleeae and their lemur dispersers reached Madagascar together, at least by very early in the Tertiary. To judge from the presence of either lemurs or these lemur-dispersed plants (or both) on each of the major outlying island groups, it seems probable that this may have happened while the now submerged Mascarene Plateau provided much easier interisland access. The existence of *Colea seychellarum* suggests that this dispersal might have preceded the northward migration of India, with subsequent extinction of other Coleeae (and lemurs?) that were formerly on India occurring as the subcontinent rafted north across dry subtropical latitudes.

It is also noteworthy that *Colea,* the most phylogenetically advanced genus of Coleeae, is the genus that has reached the Seychelles and Mauritius. This would accord with the early largely prebreakup evolution of Coleeae postulated above. In addition to a very early divergence of Coleeae, an early generic radiation would seem necessary if the tribe's most advanced genus were to be available to reach the Seychelles and Mauritius prior to their complete isolation from Madagascar. From this line of reasoning I would anticipate that fossils of the already differentiated modern Coleeae genera might be expected from the Tertiary of continental Africa [cf. the *Xylolaena* pollen recently discovered in South Africa (Coetzee & Muller, 1984)]. This line of reasoning also suggests that the Coleeae are either extremely old or that more or less direct overland connections between Madagascar and the mainland existed surprisingly late.

The lack of such "expected" taxa from continental Africa is a common pattern and has been explained as due to strong climatic deterioration of Africa through the later Tertiary and especially during the Pleistocene (e.g., Raven & Axelrod, 1974; Axelrod & Raven, 1978). This led to a floristic imbalance, with Africa often the "odd man out" (Richards, 1973) when compared with the Neotropics and tropical Asia. Many of the taxa missing or poorly represented in Africa—e.g., Lauraceae, Palmae, Orchidaceae, bamboos—occur or are better represented on the climatically buffered adjacent islands like the Canaries and Madagascar. This floristic impoverishment of Africa has been much discussed (e.g., Raven & Axelrod, 1974; Moore, 1973; Coetzee & Muller, 1984). It is interesting, however, that the resulting floristic imbalance of continental Africa as compared to Madagascar (Dejardin et al., 1973; Raven & Axelrod, 1974: 612) is much more apparent at the continental than at the local community level, a fact apparently overlooked by previous authors. At least in the central African heartland area centering in Gabon, local floras are every bit as rich as in other continents, and some of the "missing" African families like Lauraceae and Myristicaceae are fairly well represented (Gentry, 1987, 1988). It would be most instructive to have comparable data from Madagascar.

Another insight suggested by the interpretation that Coleeae probably evolved and radiated prior to completion of the separation of Madagascar and Africa is that the genera of Coleeae, despite being derived from Tecomeae ancestral stock, may be older than most of the extant African genera of Tecomeae. In this connection it is interesting that the three Tecomeae genera shared between Africa and Madagascar are the two most morphologically generalized African ones (*Fernandoa* and *Stereospermum*) plus *Rhigozum,* whose 5-staminate flowers qualify it as a likely primitive element in the tribe and family. Perhaps these were the only Tecomeae genera yet extant on the African continent when the biologically definitive separation of Madagascar and Africa took place.

From the viewpoint of conservation, it is extremely interesting that there is little correlation between overall species richness, as measured by degree grid squares, and endemism (Fig. 4). The high diversity grid squares are scattered rather haphazardly in the north central part of Madagascar while endemism is concentrated in the northern tip of the island. Only in the case of the ecologically complex Tsaratanana-Sambirano grid square does high local endemism coincide with high species richness. The other grid squares with high species numbers (i.e., 10 or more species) have only one or two locally distributed species each. Again, with the exception of the Tsaratanana-Sambirano square, the five grid squares with four or more locally endemic species are noteworthy for having generally lower species numbers than most of the surrounding areas. The northern forests, high in Bignoniaceae endemism, are the same forests in which the most striking ancient relicts, like Chloranthaceae and Winteraceae, are found. Just as in the case of the Coleeae, each relict is known from a different cloud forest, precluding a single conservational

focus. Assuming that locally endemic species are the most endangered and that other families show similar distributional patterns to those of Bignoniaceae, conservational efforts might well be at least generally focused in the north, especially in the Tsaratanana-Sambirano region, where high endemism and diversity coincide.

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DIVERSITY, DENSITY, AND INVASION IN A MAURITIAN WET FOREST[1]

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ABSTRACT

Many of the remaining indigenous forests on Mauritius (southwest Indian Ocean) are highly invaded by introduced plant species. For this paper we sampled a small, relatively undisturbed area of mature evergreen wet forest at Brise Fer (altitude ca. 550 m) for structure and floristic composition and compared this forest with a nearby area at Macabé sampled over 40 years ago. Seedling plots were also sampled to assess invasion at this stage. The forest structure at Brise Fer was found to be dense (715 indigenous individuals ≥2.5 cm dbh/0.1 ha, and 154 ≥10 cm dbh/0.1 ha), with many slow-growing, hard-wooded trees and few lianas. Species diversity was fairly high (57 indigenous species ≥2.5 cm dbh/0.1 ha, and 29 ≥10 cm dbh/0.1 ha). The sampling also revealed a high degree of invasion by exotics which, although constituting only 5% of total species diversity, accounted for 34.8% of total individuals. This invasion is dominated by two middle stratum trees, *Psidium cattleianum* var. *cattleianum* and *Ligustrum robustum* var. *walkeri*. Macabé forest is now completely degraded and choked by the same adventive species presently invading Brise Fer, and cyclones appear to have accelerated this invasion by damaging or destroying forest structure. The seedling plots at Brise Fer were found to be dominated by exotics, which comprised 97.4% of total individuals but only 20.6% of total species. Predominant exotics were *Ligustrum*, *Psidium*, and *Ardisia crenata*. Seedling data suggest that floristic composition at Brise Fer will follow the same course as at Macabé (i.e., total invasion and degradation) unless steps can be taken to check the spread of exotics.

RÉSUMÉ

Une grande partie des forêts originales encore intacte sur l'Ile Maurice (sud-ouest de l'océan indien) sont fortement envahis par des espèces introduites. Pour cet article nous avons fait des recherches dans une région relativement peu troublé de forêt humide d'arbres à feuilles persistentes à Brise Fer (alt. 150 m environ) concernant la structure et la composition floristique, et nous avons comparé cette forêt à une région proche (à Macabé) etudiée 40 ans auparavant. Des parcelles de jeunes plants ont été aussi examinées pour déterminer l'invasion à ce stade. La structure forestière à Brise Fer est dense (715 individus indigènes à ≥2,5 cm de diamètre par 0,1 ha; et 154 individus à ≥10 cm de diamètre par 0,1 ha), avec de nombreux arbres à croissance lente et de bois dur, et peu de lianes. La diversité spécifique était rélativement élevée (57 espèces indigènes à ≥2,5 cm de diamètre par 0,1 ha; et 29 espèces à ≥10 cm de diamètre par 0,1 ha). L'étude a aussi rélévé un degré élevé d'invasion d'espèces exotiques qui, bien qu'elles ne constituaient que 5% de la diversité spécifique totale, représentaient 34,8% du nombre total d'individus. Cette invasion est dominée par deux arbres qui occupent l'étage intermediaire de la forêt: *Psidium cattleianum* var. *cattleianum* et *Ligustrum robustum* var. *walkeri*. La forêt de Macabé est aujourd'hui complètement dégradée et étouffée par les mêmes espèces adventives qui envahissent Brise Fer, et des cyclones semblent avoir accéléré cette invasion en abimant ou détruisant la structure forestière. Les parcelles de jeunes plants à Brise Fer etaient dominées par les espèces exotiques qui representaient 97,4% du nombre total d'individus mais seulement 20,6% des espèces. Les espèces exotiques predominantes etaient *Ligustrum*, *Psidium* et *Ardisia crenata*. Les données sur les jeunes plants suggèrent que la composition floristique à Brise Fer evoluera de la même manière qu'à Macabé (invasion et dégradation totale) à moins qu'une action soit entreprise pour empêcher la propagation d'espèces exotiques.

Island ecosystems are notoriously fragile (Carlquist, 1965, 1974); extinctions and invasion by exotic elements are perhaps the most obvious and well documented results of man's occupancy. The Mauritius Dodo (*Raphus cucullatus*) is a classic example of the ability of humans to eliminate species in a short time (Hachisuka, 1953; Greenway, 1967). Equally significant,

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however, are the slower and more subtle changes in the equilibria of island floras invaded by introduced species. Although floristic data are abundant, data on vegetational composition and diversity (= species richness) patterns in tropical, insular plant communities are scarce (e.g., Tschirley et al., 1970; Tanner, 1977). In view of the alarming rate at which indigenous floras are being destroyed, it is imperative that such baseline information be compiled as soon as possible. If vegetational composition and diversity patterns (cf. Gentry, 1982, 1983a) are ever to be compared between different islands or between islands and the mainland, the data must be acquired now.

Mauritius, lying some 900 km east of Madagascar in the southwest Indian Ocean, is the oldest (ca. 7.8 Ma) of the three Mascarene Islands. This highly-eroded volcanic island covers 1,865 km^2 and rises to 840 m at its highest point. It was originally covered mostly by tropical evergreen and semideciduous forest inhabited by birds, bats, lizards and giant land tortoises. Since its colonization by man over 350 years ago, much of the endemic fauna has become extinct (Cheke, 1987). The indigenous vegetation has been reduced to relict patches largely confined to steep slopes, uncultivable land, ten nature reserves covering an area of 4,018 ha, and five islet reserves covering 585 ha (Anonymous, 1979). Unfortunately, most of these forest remnants are degraded, partly from direct human disturbance, and partly from invasion by the exotic plant and animal species introduced by man. Of the latter, the Russa deer (*Cervus timorensis*), the crab-eating macaque (*Macaca fascicularis*), the pig (*Sus scrofa*), and two birds, the Indian mynah (*Acridotheres tristis*) and the red-whiskered bulbul (*Pycononotus jocosus*), have become widely naturalized and have been implicated in the destruction of indigenous plant species by browsing and/or the spread of exotic plants (Vaughan & Wiéhe, 1937).

Mauritius is relatively well known floristically (Bojer, 1837; Baker, 1877; *Flore des Mascareignes,* in progress). Its plant communities were studied by Vaughan and Wiéhe (1937, 1939, 1941), who conducted vegetational sampling in several of the upland associations (i.e., above ca. 500 m on the central plateau and mountains): *Sideroxylon* wet forest, *Philippia* heath scrub, *Pandanus* marsh, cloud forest, mature high wet forest, and semideciduous dry forest. Vaughan and Wiéhe's studies generally preceded much of the recent serious invasion by exotic plant species. The floristic data base and the existence of a comparable data set over 40 years old greatly add to the value of this study.

There are few data on the dynamics of invasion of insular plant communities by introduced adventive species, a severe problem not only in the Mascarenes but also on other islands such as Hawaii (Tagawa, 1979; Vaughan, 1937). The objectives of this study were threefold: 1) to locate and sample the structure and floristic composition of a relatively undisturbed core habitat (= climatic climax) area of mature upland wet forest; 2) to compare it with the site at Macabé sampled by Vaughan & Wiéhe (1937, 1941) more than 40 years ago and now highly invaded by exotics; and 3) to survey a number of seedling plots to assess regeneration of both indigenous and exotic species.

The Study Site

The original upland climax vegetation of Mauritius consisted for the most part of tropical lower montane moist and wet forest (sensu Lorence, 1978). Other vegetation types include *Pandanus* associations in marshy areas, *Philippia* heath scrub formations on unweathered laterite, patches of cloud forest on the highest peaks, semideciduous dry forest in the rain shadow regions, and palm savanna along the coast (see Vaughan & Wiéhe, 1937; Lorence, 1978, for more details). In optimal upland sites, sheltered from direct winds and with deep soils, the climatic climax is usually a moist or wet "high" forest with four distinct strata like the one at Macabé plateau (altitude 550 m, annual precipitation ca. 3,200 mm) studied by Vaughan & Wiéhe (1937, 1941, 1947).

Macabé forest now appears to be irreversibly degraded due to intense invasion by weedy exotic plant species. Severe cyclone damage suffered in 1960 apparently accelerated the invasion rate (Vaughan, 1968). Many of these exotics have soft wood or leaves and are not well adapted to withstand cyclones. Consequently, most inhabit the forest's lower strata, where they drastically change the forest structure and species composition even without human interference. Now the original understory at Macabé has virtually disappeared. The only young indigenous plants to be found are in a weeded plot (pers. obs.; W. Strahm, pers. comm.). Beneath the strata of mature, dying, and dead trees a dense, often impenetrable thicket of

TABLE 1. Some adventive plant species invading indigenous upland plant formations in Mauritius. Equivalent names used by Vaughan & Wiéhe (1937, 1941) given in parentheses.

Family	Species	Local Name	Country of Origin	Estimated Date of Introduction	Distribution in Upland Mauritius
Euphorbiaceae	*Homalanthus populifolius* R. Grah.	—	E. Indies, Malaya	btwn. 1877 & ca. 1937	S central plateau (esp. Mt. Cocotte)
Lauraceae	*Litsea monopetala* (Roxb.) Pers.	Yati; Bois d'oiseaux à grandes feuilles	E. Indies, Malaya	ca. 1816	most areas
Malpighiaceae	*Hiptage benghalensis* Kurz	Liane de cerf	Burma, India	ca. 1785	escarpments of western mtns.
Melastomataceae	*Ossaea marginata* (Desr.) Triana	—	Brazil	btwn. 1877 & 1937	most areas
Myrsinaceae	*Ardisia crenata* Sims	Arbre à noël	China	early 1800s	most areas
Myrtaceae	*Psidium cattleianum* Sabine var. *cattleianum* (forms with both red and yellow fruits occur)	Goyave de Chine rouge; Goyave de Chine jaune; red & yellow Strawberry Guava	Brazil (via China)	by ca. 1822	all areas
Oleaceae	*Ligustrum robustum* Blume var. *walkeri* (Decne.) Mansfr. (*L. walkeri* Decne.)	Privet	Ceylon	1904	most areas
Rosaceae	*Rubus moluccanus* L. (*R. roridus* Lindl.)	Piquant lou-lou	Himalayas to Australia (prob. via Madagascar)	1828	most areas
Strelitziaceae	*Ravenala madagascariensis* J. F. Gmel.	Ravenale; Arbre à voyageur	Madagascar	ca. 1785	E mountain ranges; S central plateau

exotics has developed which chokes out any indigenous regeneration. These exotics include *Ligustrum robustum* var. *walkeri* and *Psidium cattleianum* var. *cattleianum*, both small trees; *Rubus moluccanus*, an armed vining raspberry; *Ossaea marginata*, a wiry shrub; and *Ardisia crenata*, a miniature tree 30–60 cm tall. Country of origin and probable date of introduction of these and other highly invasive exotics in upland Mauritius are given in Table 1.

We were interested in studying a site where disturbance and invasion were minimal in order to compare floristic composition and density and to assess invasion by exotics. Since Macabé is so degraded, we were forced to find another site for evaluation of the early stages of the invasive process. A site was selected in a sheltered valley just east of Piton Brise Fer, on the western extremity of the island's central plateau (20°22′37″S, 57°25′36″E) at ca. 550 m altitude. Except for a forestry road leading to the area and two small tracks through and adjacent to the site, the study area was undisturbed, with no signs of cutting.

Due to its more westerly location near the rain shadow, Brise Fer is somewhat drier (annual precipitation ca. 2,400 mm) than Macabé. The driest months are from mid September to December, although no true rainless season exists. Following Köppen's classification, the climate at Brise Fer is temperate with no dry season (CFa), transitional to humid tropical with a winter dry season (AW1) (Halais & Davy, 1969). According to

FIGURE 1. Brise Fer wet forest.—A. Forest profile outside of study area showing low, dense interlocking canopy of upper stratum with emergent *Syzygium glomeratum*, the lower and mid strata highly invaded by

Thornthwaite's classification for potential evapotranspiration, it is super-humid mesothermal, transitional between his ArB'3a' and ArB'4a' climatic formulas (Halais & Davy, 1969). Annual temperatures are unavailable for Brise Fer, but are presumably several degrees higher than at Macabé (mean annual temperature 20°C; lowest means 14–14.6°C in July–August; highest means 23.5–26°C in January–February; mean diurnal variation 6°C; Vaughan & Wiéhe, 1941, 1947). The sample area consists of a flat valley bottom and adjacent steep slope rising some 20–25 m. The soil is deep and dark brown here, and of the humic ferruginous latosol type, although nearby areas have thin, yellowish or reddish lithosols over a hard, unweathered laterite bedrock (Parish & Feillafé, 1965).

Methods

In 1980, ten transects of 50 × 2 m (giving a total of 1,000 m² or 0.1 ha) were laid out and all individuals ≥2.5 cm dbh (diameter at breast height) and rooted therein were recorded (Lorence & Sussman, 1986). As documented by Gentry (1982, 1986), samples of 1,000 m² of tropical forest give an adequate idea of species richness and diversity when individuals ≥2.5 cm dbh are recorded. Although Gentry (1982) estimated that areas of over one km² may be necessary for a species/area curve to asymptote in some neotropical continental forests, our curve showed considerable leveling off at 1,000 m². This suggests that at this site most of the species present were included. Plant identifications were made by the first author using habit and bark characters in addition to vegetative, flowering and/or fruiting material. Most material was confidently identified in the field. Specimens of problematic individuals were collected for later identification at the Mauritius herbarium (MAU). Voucher specimens are deposited at MAU and in the Missouri Botanical Garden herbarium (MO).

Ten seedling plots of 2 × 2 m each were selected at random, one per transect, making a total of 40 m². In these, all seedlings and young plants of angiosperms less than 2.5 cm diam. were sampled, excluding herb species.

Most names employed herein are from Baker (1877), except where more recent revisions or family treatments for *Flore des Mascareignes* exist, published or in manuscript form. In the latter cases, equivalent names employed by Vaughan & Wiéhe are given in parentheses where different from ours.

Results and Discussion

Transects

A. *Composition.* The forest at Brise Fer may be classified as lower montane moist or wet forest (Lorence, 1978; Lorence & Sussman, 1986). It displays a peculiar physiognomy that seems to characterize Mauritian evergreen forests, and those of the Mascarene Islands in general, as being dense (Fig. 1A, B, D) and composed of slow-growing, hard-wooded trees with very few lianas (Vaughan & Wiéhe, 1937, 1941; Wiéhe, 1949; Cadet, 1977). The rich flora includes a number of endemic taxa. Both forests are evergreen, and the only deciduous species present is *Ochna mauritiana*, an occasional second stratum tree. Another striking physiognomic feature shared by both forests is the presence of buttresses and large surface roots. Both *Labourdonnaisia glauca* and *Syzygium glomeratum* are conspicuously buttressed basally (Figs. 1A, B; 2A), whereas *Canarium paniculatum* (fig. 2B), *Mimusops maxima*, and *Sideroxylon cinereum* frequently have large surface roots extending for considerable distances along the forest floor as noted by Vaughan & Wiéhe (1941).

Although similar to that occurring at Macabé in many respects, the forest at Brise Fer differs physiognomically in lacking the open canopy of emergent species found there (i.e., the first, or α-mesophanerophyte, stratum of Vaughan & Wiéhe, 1937). In contrast, the upper stratum at Brise Fer is mostly uniform in height, closed, and somewhat lower, only 14–16(–18) m tall. Occasional large individuals of *Labourdonnaisia glauca* or *Syzygium glomeratum* emerge several meters above the main canopy (Fig. 1A, B). We

←
Psidium cattleianum var. *cattleianum*.—B. Somewhat more open forest along road to study area showing two tall *Labourdonnaisia glauca* trees left of center, the lower and mid strata dominated by *Psidium cattleianum* var. *cattleianum*.—C. Close-up of *Psidium cattleianum* var. *cattleianum* dominating lower and mid strata along roadside.—D. Path through interior of forest at study area showing relatively uninvaded area on slope. Note dense stocking and slender boles of indigenous trees, scarcity of epiphytes and lianas. Photos taken in July 1984.

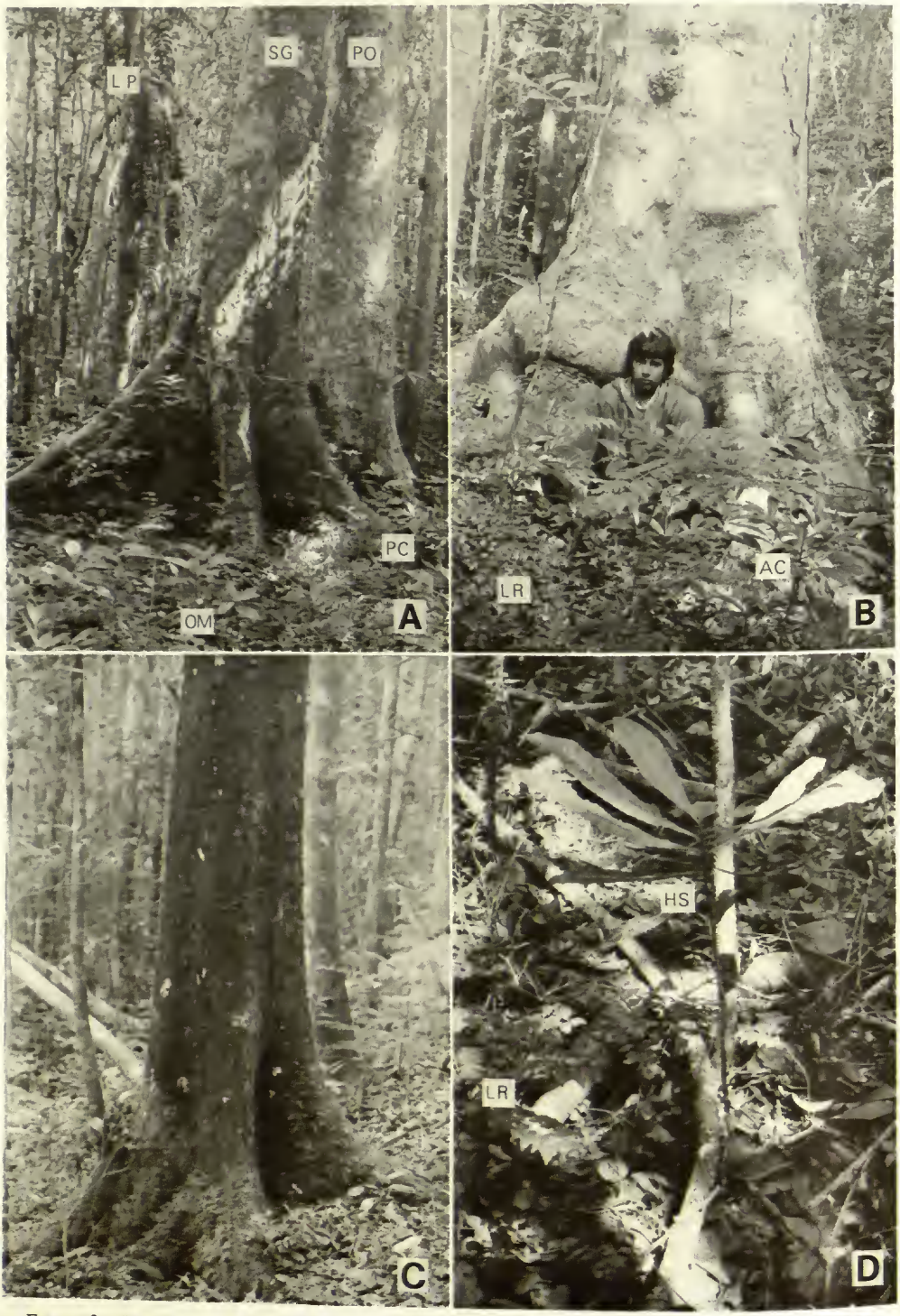

FIGURE 2. Brise Fer wet forest, some component species.—A. Boles of *Sideroxylon grandiflorum* (SG) with buttresses, and *Protium obtusifolium* (PO). Note hemiepiphytic fern *Lomariopsis pollicina* (LP) and dense

have defined canopy species, listed in Table 2, as those whose trunks exceed 25 cm dbh, since at this site this diameter generally separates canopy species from those restricted to the middle stratum. Two occasional canopy species, *Sideroxylon cinereum* and *Calophyllum tacamahaca,* were recorded from the middle stratum in our sample. The canopy species occur in different size classes (Table 2), suggesting regeneration in the past (but also see the seedling data).

The floristic composition of the Brise Fer forest is very similar to that of the forest at Macabé. The only two canopy species recorded at Macabé but not at Brise Fer are *Sideroxylon grandiflorum* DC. (Fig. 2A) and *Tambourissa sieberi* (Tulasne) A.DC., and the former occurs outside our plots. Three rare species with extremely restricted distributions in Mauritius, *Elaeocarpus integrifolius* Lam., *Zanthoxylum heterophyllum* (Lam.) Smith, and *Weinmannia tinctoria* Sw., are present at Brise Fer but were not recorded at Macabé; none of these was represented in our plots. However, the most abundant canopy species at Brise Fer is the Mauritius black ebony, *Diospyros tessellaria* (Fig. 2C), which is absent at Macabé. The species is characteristic of drier areas, suggesting that Brise Fer represents a transition zone.

All of the canopy species are also found in the middle stratum (second, or β-mesophanerophyte, stratum of Vaughan & Wiéhe), along with many species restricted to this layer (Table 3). We were not able to discern a clear separation of the β-mesophanerophyte stratum (8–14 m) from the third, or microphanerophyte, stratum (2–8 m) recognized by Vaughan & Wiéhe at Macabé. Therefore we have combined these two elements as a second, or middle, stratum ranging from ca. 2–15 meters tall. Middle stratum species are given in Table 3. These species almost never exceed 25 cm dbh. The exception is one individual of *Grangeria borbonica* in the 30–35 cm diameter category (not included in Table 3).

The majority of middle stratum taxa were also present at Macabé, but that site contains several additional species not occurring at Brise Fer. Only a few Brise Fer species are not recorded for Macabé, i.e., both *Badula* species, *Eugenia pollicina, Syzygium obovatum,* and *Doratoxylon apetalum* (Poir.) Radlk. Three middle stratum species are present at Brise Fer but not recorded in our transects. These are *Badula multiflora* A. DC., *Chasalia capitata* DC., and *Doratoxylon apetalum.* Species appearing only in the seedling plots but not in the transects are *Geniostoma borbonicum* Spreng. (indigenous) and the exotics *Litsea monopetala, Ossaea marginata* (Fig. 2A), and *Ravenala madagascariensis.*

Although obviously much less invaded than its counterpart at Macabé, the entire second stratum at Brise Fer is pervaded by the two exotic trees, *Psidium cattleianum* var. *cattleianum* (with 282 individuals/1,000 m^2) and *Ligustrum robustum* var. *walkeri* (97 individuals/1,000 m^2)

TABLE 2. Number of individuals of tree species characteristic of the upper stratum of Brise Fer in transects totaling 1,000 m^2 for three different size classes. Equivalent names used by Vaughan & Wiéhe (1937, 1941) in parentheses.

Species	Size Classes (dbh) 2.5–10 cm	10–25 cm	>25 cm
Diospyros tessellaria	29	24	6
Labourdonnaisia glauca	12	11	6
Protium obtusifolium	1	7	6
Mimusops maxima	1	7	6
Syzygium glomeratum (*Eugenia glomerata* Lam.)	6	9	4
Elaeodendron orientale	19	2	1
Nuxia verticillata	2	0	1
Securinega durissima	48	2	1
Canarium paniculatum (*C. mauritianum* Blume)	6	4	1
Sideroxylon cinereum (*S. bojerianum* A.DC.)	1	4	0
Calophyllum tacamahaca (*C. inophyllum* L. var. *tacamaha* (Willd.) R. E. Vaughan)	1	0	0
Total	126	70	32

←

stocking of exotics in ground flora, including *Ossaea marginata* (OM) and *Psidium cattleianum* var. *cattleianum* (PC).—B. Bole of large *Canarium paniculatum* with surface roots. Note dense stocking of exotics in ground flora, including *Ardisia crenata* (AC) and *Ligustrum robustum* var. *walkeri* (LR).—C. Bole of *Diospyros tessellaria.* Note scarcity of epiphytes and sparse ground flora.—D. Ground flora with seedlings of the indigenous liana *Hugonia serrata* (HS) and the exotic *Ligustrum robustum* var. *walkeri* (LR). Photos taken in July 1984.

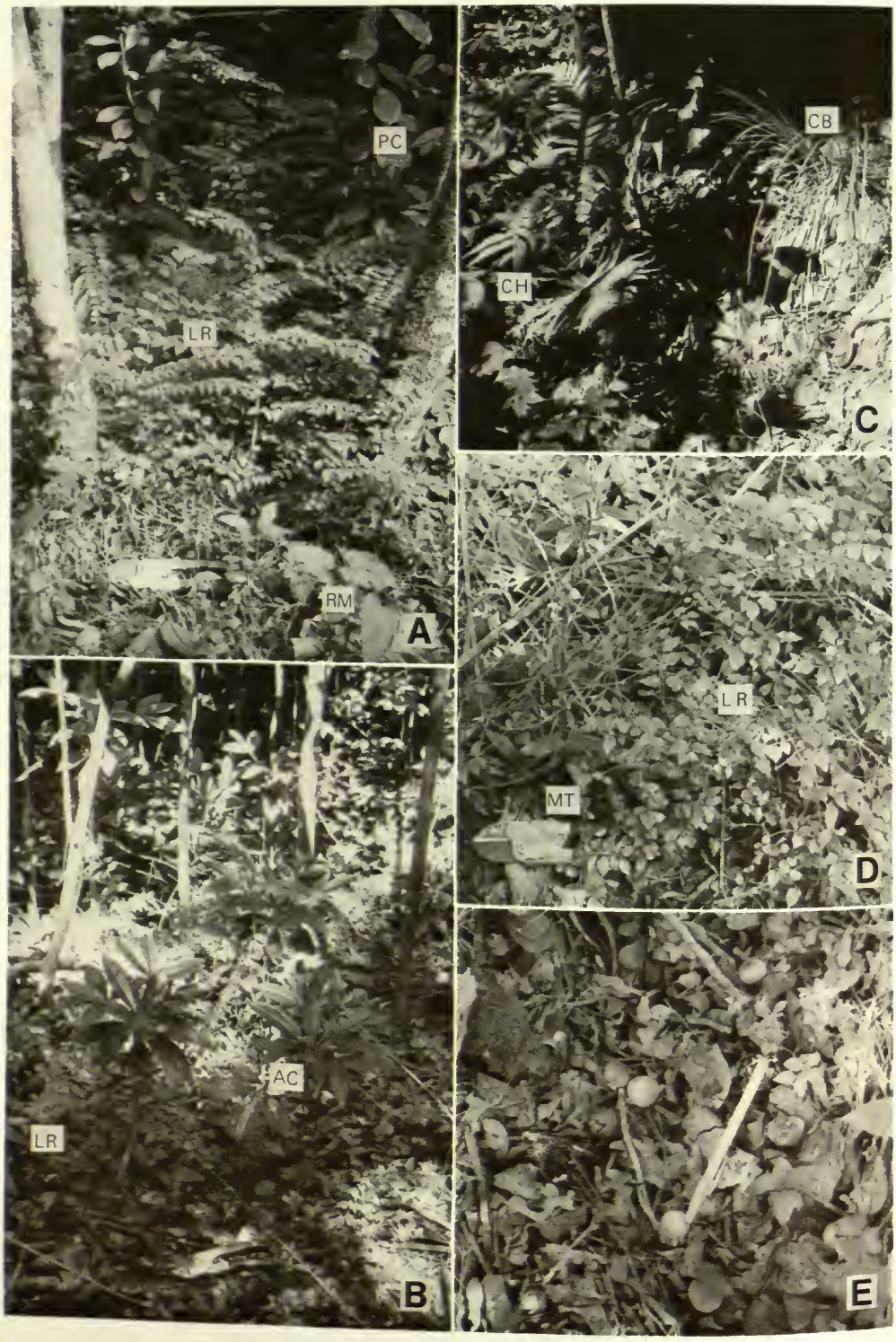
PC
LR
RM
A
CB
CH
C
LR
MT
D
AC
LR
B
E

TABLE 3. Some middle stratum tree species occurring at Brise Fer, followed by density/1,000 m². Only individuals 2.5–25 cm dbh are included. Equivalent names used by Vaughan & Wiehe (1937, 1941) given in parentheses.

Species	Density	Species	Density
Erythrospermum monticolum var. *pyrifolium* (*E. mauritianum* Baker)	117	*Eugenia elliptica*	5
Tabernaemontana mauritiana (*Conopharyngia mauritiana* (Poir.) R. E. Vaughan)	58	*Ludia mauritiana*	5
Securinega durissima	51	*Erythroxylon laurifolium*	4
Monimiastrum globosum (prob. *Eugenia orbiculata* Lam.)	26	*Cordemoya integrifolia* (*Mallotus integrifolius* Muell.-Arg.)	4
Erythrospermum monticolum var. *amplifolium* (*E. amplifolium* Thouars)	23	*Homalium* cf. *paniculatum*	4
Gaertnera psychotrioides	22	*Badula sieberi*	4
Fernelia buxifolia	21	*Casaeria coriacea* (*C. fasciculata* Bojer)	3
Antidesma madagascariense (*A. longifolium* Bojer)	19	*Molinaea* sp.	3
Lautembergia neraudiana ("Bois caf-caf")	19	*Syzygium* sp.	3
Memecylon ovalifolium (*M. angulatum* Reich.)	18	*Erythroxylon longifolium* (*E. mauritianum* Baker)	2
Aphloia theiformis	17	*Ocotea* sp.	2
Protium obtusifolium	14	*Tambourissa ficus*	2
Pleurostylia leucocarpa	14	*Tambourissa peltata* (prob. "Tp")	2
Memecylon trinerve	12	*Antirhea verticillata*	2
Eugenia pollicina	12	*Apodytes dimidiatum* (*A. mauritianum* Planch.)	1
Grangeria borbonica	8	*Allophyllus cobbe* (*A. integrifolius* Blume)	1
Ochna mauritiana	7	*Eugenia* sp.	1
Syzygium commersonii (prob. *Eugenia venosa* Lam.)	7	*Psiloxylon mauritianum*	1
Xylopia richardii	6	*Syzygium obovatum*	1
		Olea lancea	1
		Bertiera zaluzania	1
		Rubiaceae sp. A.	1
		Indet. sp. A	1
		Indet. sp. B	1
		Total 44	526

(Figs. 1, 3). These are the first and third most abundant species at Brise Fer respectively, the second most abundant being the endemic *Erythrospermum monticolum* var. *pyrifolium*.

The understory, or third stratum (the fourth, or nanophanerophyte, stratum of Vaughan & Wiehe), defined as plants under two meters tall, consists of juvenile trees and treelets of species from the upper two strata. Many of these are exotics, and no true shrubs are present. Vines (lianas) are few, both in terms of individuals and species (Table 4), and include only the following four species, in decreasing order of abundance: *Hugonia serrata* (9), *Cnestis glabra* (8), *Scutia myrtina* (3), and *Danais fragrans* (2). Three of these four vine species were also present at Macabé. *Danais* is absent from Macabé, but an additional species, *Clematis mauritiana* Lam., occurs there. Palms are extremely scarce in Mauritius and are absent from Brise Fer. They were once much more common, but most of the species with edible hearts have been collected to near extinction in the wild.

The Mauritian ground flora, as noted by

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FIGURE 3. Brise Fer wet forest, ground flora.—A. Forest margin invaded by the exotics *Ligustrum robustum* var. *walkeri* (LR), *Psidium cattleianum* var. *cattleianum* (PC), and *Rubus moluccanus* (RM).—B. Heavily shaded forest interior with exotics, *Ardisia crenata* (AC), *Ligustrum robustum* var. *walkeri* (LR). Most of the small tree stems are *Psidium cattleianum* var. *cattleianum*.—C. Same, with some indigenous components, *Carex brunnea* (CB) and *Cristella hilsenbergii* (CH).—D. Same, an indigenous seedling, *Memecylon trinerve* (MT), among those of *Ligustrum robustum* var. *walkeri* (LR).—E. Fallen fruits of *Psidium cattleianum* var. *cattleianum* littering the forest floor. Photos taken in July 1984.

TABLE 4. Diversity and density at Brise Fer for individuals ≥2.5 cm dbh per 1,000 m².

	Diversity: Number of Taxa and Life Forms/1,000 m²														
	Families		Species		Vines			Shrubs			All Trees			Large Trees (≥10 cm dbh)		
Status	No.	% Total	No.	% Total	No.	% Vines	% Total	No.	% Shrubs	% Total	No.	% All Trees	% Total	No.	% Lg. Trees	% Total
Indigenous	25	89.3	57	95.0	4	80.0	6.7	0	0	0	53	96.4	88.3	29	93.5	48.3
Exotic	3	10.7	3	5.0	1	20.0	1.6	0	0	0	2	3.6	3.3	2	6.5	3.3
Total	28	100.0	60	100.0	5	100.0	8.3	0	0	0	55	100.0	91.6	31	100.0	51.6

	Density: Number of Individuals/1,000 m²												
	Individuals		Vines			Shrubs			All Trees			Large Trees (≥10 cm dbh)		
Status	No.	% Total	No.	% Vines	% Total	No.	% Shrubs	% Total	No.	% All Trees	% Total	No.	% Lg. Trees	% Total
Indigenous	715	65.2	20	91.7	1.8	0	0	0	695	64.7	63.4	154	98.7	14.0
Exotic	381	34.8	2	8.3	0.2	0	0	0	379	35.3	34.6	2	1.3	0.2
Total	1,096	100.0	22	100.0	2.0	0	0	0	1,074	100.0	98.0	156	100.0	14.2

Vaughan & Wiéhe (1937) for Macabé, is sparse and low in diversity, perhaps resulting from heavy shading (Fig. 3A) in these unusually dense forests. It consists of the following species: the tiny exotic treelet *Ardisia crenata, Carex brunnea* Thunb., *Oplismenus hirtellus* (L.) Beauv., *Pilea urticifolia* Blume, *Phajus tetragonus* (Thouars) Reichb., and a number of pteridophytes including *Selaginella concinna* Spring, *Ctenitis crinita* (Lam.) Ching var. *crinita, Cristella hilsenbergii* (Presl) Holtt., and *Heterogonium cyatheifolium* (Desv.) Tard. The juvenile phase of *Lomariopsis pollicina* (Willem.) Mett. is particularly abundant, as are the invasive exotics and their seedlings. Dense stands of the wiry-stemmed exotic *Ossaea marginata* are also encountered in many areas (Fig. 2A).

There are slightly more pteridophytes at Brise Fer than at Macabé (38 species vs. 32), although a number are extremely rare and localized, such as the epiphytes *Davallia chaerophylloides* (Poir.) Steud. var. *mauritiana* (Hook.) Tard., and *Drynaria willdenowii* (Bory) Moore (Lorence, 1978). Tree ferns are absent at Brise Fer, although two species of *Cyathea* occur at Macabé. Epiphytes in the study area are generally sparse, the commonest being ferns. A few species of *Peperomia* and orchids such as *Bulbophyllum* spp. are the only flowering epiphytes encountered here.

Hemiepiphytes that ascend trees for several meters include *Lomariopsis pollicina* (the most frequent), *Piper borbonense* Cas., and *Blechnum attenuatum* (Sw.) Mett. var. *attenuatum*. Covering the bases and roots of trees are various mosses, hepatics, and the filmy ferns *Hymenophyllum inaequale* Desv. and *Trichomanes bipunctatum* Poir.

B. *Diversity.* Figures for both diversity and density at Brise Fer (excluding exotics) correspond closely with the 1941 values for Macabé. In both Mauritian forests diversity is considerably lower and density higher than in comparable continental forests (Gentry, 1982, 1986). Our sample area of 1,000 m^2 (summarized in Table 4; see also Lorence & Sussman, 1986) contained 1,096 individuals (715 indigenous; 381 exotic) and 60 species (57 indigenous; 3 exotic) $\geq$2.5 cm dbh.

However, the current structure of the Mauritian forests is greatly modified by the numerous exotics. As noted, Macabé is now little more than a thicket of exotics. At Brise Fer exotics account for only 5% of the total species diversity, but constitute 34.8% of individuals. Of the three exotic species present in the transects, guava and privet are the first and third most abundant species, respectively comprising 25.7% and 8.9% of the total density. Both are small trees of the middle stratum reaching 4–6 m and virtually all are under 10 cm dbh (Lorence & Sussman, 1986). The third forest exotic, *Hiptage benghalensis*, is a vine of rare occurrence discussed below.

Twenty native species were represented in our sample by 10 or more individuals. Among the indigenous species, the mid-stratum tree *Erythrospermum monticolum* var. *pyrifolium* is the most abundant (10.7% of the total individuals). Other important indigenous species include: *Diospyros* (5.5%) and *Tabernaemontana* (5.3%), followed by *Securinega* (4.7%), *Labourdonnaisia* (2.6%), *Monimiastrum* (2.4%), *Erythrospermum monticolum* var. *amplifolium* (2.1%), *Elaeodendron* and *Gaertnera* (both 2.0%), *Fernelia* (1.9%), *Antidesma, Lautembergia,* and *Syzygium glomeratum* (all 1.7%), *Memecylon ovalifolium* and *Aphloia* (both 1.6%), *Mimusops, Protium,* and *Pleurostylia* (all 1.3%), *Eugenia pollicina* and *Memecylon trinerve* (both 1.1%), and *Canarium* (1.0%). The most important families, as judged by number of species, are: Myrtaceae (9), Rubiaceae (7), Flacourtiaceae (5 plus 2 varieties), Euphorbiaceae (4), and Sapotaceae (3).

Although species diversity in neotropical core habitats generally shows a strong correlation with precipitation (Gentry, 1982), this was not manifest between the two Mauritian sites, perhaps because the differences in rainfall are not great (Table 5). Diversity of indigeous species $\geq$10 cm dbh is very similar at Brise Fer (29 spp./1,000 m^2) and Macabé (24–32 spp. for ten 100 m^2 transects; average 27). However, the actual value of 52 species in the sampled hectare at Macabé is higher than the anticipated 39 per hectare for Brise Fer (calculated from the formula of Evans et al., 1955). Both forests' values are similar to figures for trees $\geq$10 cm dbh in 0.1 ha samples of neotropical lowland forests (moist forest average 28 spp., wet forest average 30 spp.; Table 5). However, the number of species of small trees ($\leq$10 cm dbh) in the Mauritian forests is much lower than in the neotropical forests, despite the much greater density on Mauritius. Brise Fer supports only about half the number of species $\geq$2.5 cm dbh per 1,000 m^2 (60) as neotropical continental sites with comparable precipitation (moist forest average 109 spp.; wet forest average 143 spp.; Gentry, 1982). Liana diversity at Brise

TABLE 5. Comparison of species diversity and density between some tropical continental and insular moist and wet forest sites.

Site	Plot Size (ha)	Number of Species dbh (lower limit) 2.5 cm	Number of Species dbh (lower limit) 10 cm	Number of Individuals dbh (lower limit) 2.5 cm	Number of Individuals dbh (lower limit) 10 cm	Precipitation (mm)	Altitude (m)	Source
Neotropical continental moist forest average (4 sites)	0.1	109	28	314	41	1,830–2,433	<300	Gentry, 1982
Neotropical continental wet forest average (4 sites)	0.1	143	30	349	51	2,650–3,000	<300	Gentry, 1982
Upper Amazonian forest average (10 sites)	0.1	180	44	398	67	2,000–4,000	<400	Gentry, 1987
Brise Fer, Mauritius (excluding exotics)	0.1	57	29	715	154	2,400	600	Lorence & Sussman, 1986
Bon Courage, Mauritius	0.1	47	10	762	166	2,400	200–260	Lorence & Sussman, 1986
Macabé, Mauritius	1.0	—	52	—	1,710	3,200	660	Vaughan & Wiéhe, 1937, 1941
Macabé, Mauritius	0.1	—	24–32 (av. 27)	—	126–214 (av. 171)	3,200	660	Vaughan & Wiéhe, 1937, 1941
Maricao, Puerto Rico	0.9	105	60	2,112	—	2,030	700	Tschirley et al., 1970
Luquillo, Puerto Rico	1.4	85	61	3,265	—	2,690	540	Tschirley et al., 1970
Rivière Pirogue, New Caledonia	0.1	150	50	664	124	2,200	350–400	Gentry, pers. comm.
Round Hill, Jamaica	0.1	56	35	559	133	1,200	350	Kapos, 1982
Mor Ridge, Jamaica	0.1	—	16	—	ca. 490	3,000	1,550	Tanner, 1977
Mull Ridge, Jamaica	0.1	—	34	—	ca. 520	3,000	1,550	Tanner, 1977
Wet Slope, Jamaica	0.1	—	34	—	ca. 360	3,000	1,550	Tanner, 1977
Gap Forest, Jamaica	0.1	—	27	—	ca. 270	3,000	1,550	Tanner, 1977

Fer (4 indigenous species) and density (22/1,000 m^2) are much lower than in continental areas (average 25 spp. and 55 individuals per 1,000 m^2 for tropical moist forest; 32 spp. and 65 individuals for tropical wet forest; Gentry, 1982). Likewise, Vaughan & Wiéhe (1937, 1941) record only four liana species per hectare at Macabé. Gentry (1983a) notes that relative scarcity of lianas is a common theme on islands and suggests that this may be due to the fact that relatively few liana species possess efficient long-distance dispersal mechanisms.

C. *Density.* Comparison of density figures from various published reports is often difficult because of differences in sampling techniques. Further complications may arise in terminology, and what may be considered lowland in a continental sense (i.e., below 1,000 m alt.) is actually montane or "upland" on islands such as Mauritius whose maximum altitude is only 840 m. Nevertheless, it is instructive to compare density at the Mauritian sites with existing lowland data for other islands and continental areas.

For Macabé, Vaughan & Wiéhe (1941) obtained figures of 126–214 individuals ≥10 cm dbh for ten 1,000 m^2 transects, as well as a density of 17,710 per hectare for juveniles and seedlings less than 1 cm diam. and 50 cm high. Our figures for Brise Fer were 713 individuals ≥2.5 cm dbh and 154 individuals ≥10 cm dbh per 1,000 m^2. Large (≥10 cm dbh) tree densities are

comparable for both forests, and both fall within the range for other lowland insular forests, which vary widely (Table 5). For example, in a Jamaican lowland dry forest at Round Hill, plots totaling 1,000 m² had a density of 559 individuals ≥2.5 cm dbh and 133 ≥10 cm dbh (Kapos, 1982). In contrast, two moist forests in Puerto Rico had estimated densities of only 233 and 235 individuals ≥2.5 cm dbh/1,000 m², respectively (extrapolated from Tschirley et al., 1970), whereas a third wet forest site there had an estimated density of 87 trees ≥10 cm dbh/1,000 m² (Smith, 1970).

A series of neotropical continental lowland moist forests averaged 314 individuals ≥2.5 cm dbh/1,000 m², and wet forests are only slightly higher, with 349 individuals (Gentry, 1982). In addition, a series of 10 Amazonian sites averaged 398 individuals ≥2.5 cm dbh (Gentry, 1987). All these values are within the range for insular forests.

The reputedly high insular tropical forest densities are most manifest in large (≥10 cm dbh) trees, and our data for Brise Fer, like Vaughan & Wiéhe's (1941) for Macabé, are among the highest reported in the world. Figures for large trees per 1,000 m² at other lowland insular sites range from only 85 at Luquillo wet forest in Puerto Rico (Table 5) to 124 at Rivière Pirogue, New Caledonia (Gentry, pers. comm.), and 133 in a Jamaican dry forest at Round Hill (Kapos, 1982). All of these are considerably higher than the average of 41 (range 38–52) for neotropical continental lowland moist forest, and 51 (range 42–60) for wet forest recorded by Gentry (1982), or Gentry's (1987) ten-site Amazonian forest series which averaged 66.8 trees ≥10 cm dbh per 0.1 ha. Altitude is probably a factor influencing large tree density, at least on islands, as data for montane cloud forest (alt. 1,550 m, precipitation 3,000 mm) in Jamaica show large tree densities that range from 270 to 520 per 1,000 m² at four sites (Tanner, 1977).

We know of no mechanism that has been proposed to explain the relatively high densities for large trees in tropical insular floras. However, the Mascarene and Caribbean islands and New Caledonia for which data are available are subjected to intense tropical cyclones (hurricanes) almost every year, and this may constitute part of the explanation. In Mauritius the forest canopy is low (15–20 m) (Fig. 1A, B), and most of the canopy trees have hard wood, thick sclerophyllous leaves, and slow growth rates, which appear to be adaptations to resist cyclonic winds (Vaughan & Wiéhe, 1937; Brouard, 1967). Germination rates are also low, and this combination of factors explains their inability to compete with vigorous, fast-growing exotic species that can thrive in their shade and shelter (but which are also severely damaged by cyclones). Presumably, a denser stocking of the forests and the resulting thick, interlocking canopy decrease the likelihood of damage during cyclonic onslaughts where winds may gust up to 240–320 km/hr.

A second possible explanation is related to the scarcity of lianas which, perhaps for dispersal reasons, are generally neither abundant nor diverse on many islands (cf. Gentry, 1983a). Because the tree canopies are not tied together by lianas as in many continental forests (Gentry, 1983b), the insular forests may have compensated by developing thicker interlocking canopies as a strategy for protection against cyclones.

D. *Pollination and dispersal strategies.* Over half (60%) of the total 60 species recorded in the transects at Brise Fer (Fig. 4; Lorence & Sussman, 1986) flower massively with small tan, white, greenish- or yellowish-white flowers that produce a pleasant fragrance and small nectar reward ("inconspicuous" sensu Gentry, 1982). These are presumably pollinated by a variety of small generalist insects, including flies, bees, lepidopterans, and possibly small beetles. A lesser number (31.7%) produce larger, often solitary, white, yellowish, pinkish or purplish flowers that are frequently strongly scented and may contain a larger nectar reward ("conspicuous" sensu Gentry, 1982). This latter group includes *Eugenia, Chasalia, Gaertnera, Diospyros, Monimiastrum, Syzygium, Tabernaemontana, Tambourissa,* and *Xylopia.* Probable pollinators of this group include larger flies such as syrphids, larger bees, lepidopterans, and even beetles. The two species of *Tambourissa* occurring at Brise Fer, for example, are pollinated by large flies including syrphids (Lorence, 1985). In addition, several of the indigenous birds are nectar-foraging and could be effective as pollinators. The only possible case of anemophily (1.7%) may be in *Cordemoya integrifolia* (Euphorbiaceae), which has greenish, apetalous unisexual flowers with numerous stamens and long, branched styles, apparently unscented and without nectar. Field observations of *Cordemoya* are lacking, however, and alternatively its pollination may be affected by small insects, as it is an understory tree ex-

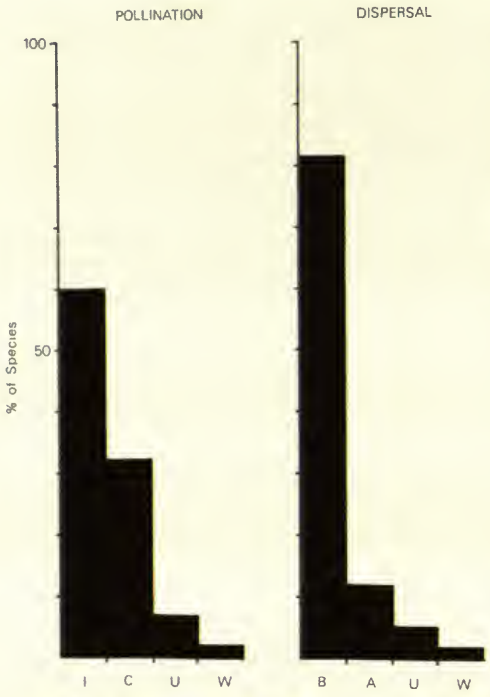

FIGURE 4. Pollination and dispersal modes for species ≥ 2.5 cm dbh in a 1,000 m² sample of evergreen wet forest at Brise Fer, Mauritius (A, autochorous; B, bird/bat; C, conspicuous; I, inconspicuous; U, unknown; W, wind).

posed to little wind. For the remaining 6.6% the mode of pollination is uncertain.

Most of the species at Brise Fer (81.6%) have fleshy red, yellow or bluish-black endozoochorous fruits adapted for dispersal by birds and/or bats (Fig. 4; Lorence & Sussman, 1986), a phenomenon common in mainland tropical evergreen moist or wet forests. Mauritius harbors one species of fruit bat, *Pteropus niger,* which is also nectar-foraging (Cheke & Dahl, 1981) (a second is now extinct), and two species of insectivorous bats, the island's only native mammals. Originally about 35 indigenous bird species (23 endemics) inhabited Mauritius; 14 of these are now extinct (Hachisuka, 1953; Greenway, 1967; Cheke, 1987). Thus, the high incidence of bird- and bat-dispersed species accords well with present-day ecology as well as the original need for long-distance colonization. Six species (11.7%) are apparently autochorous but only one (1.7%) is wind dispersed (*Hiptage benghalensis,* an exotic vine). Wind-dispersed species, which tend to be poor at long-distance dispersal (Carlquist, 1965, 1974), are much more common in neotropical mainland, seasonally deciduous, dry forests and scarce in evergreen forests (Gentry, 1982). The low incidence of wind dispersal in Mauritian wet forests would be predicted on either grounds. Of the four indigenous lianas, two (*Cnestis glabra* and *Hugonia serrata*) are presumably bird dispersed. *Scutia myrtina* may either be autochorous or zoochorous, and *Danais fragrans* is probably autochorous. Some of the bird- and bat-dispersed fruits, especially guava, are being eaten and presumably dispersed by the introduced crab-eating macaque (*Macaca fascicularis*), as are some of the indigenous ebonies, Sapotaceae, Myrtaceae, and others. Most of the remaining exotic species at Brise Fer, including *Ardisia, Ligustrum, Litsea, Ossaea,* and *Rubus,* have small, fleshy fruits presumably dispersed by birds. Dispersal mechanisms are unknown for 5% of the species.

SEEDLING PLOTS

Degree of invasion by adventive species varies considerably between islands. The parameters involved are poorly understood but obviously include vigor and preadaptation of the exotics to particular insular microclimates in relation to the vigor and fecundity of the indigenous species occupying these habitats. The floras of some islands seem relatively resistant to invasion by adventives. For example, Tschirley et al. (1970) noted that *Calophyllum calaba* Jacq. was the only naturalized component of Maricao forest in Puerto Rico, even though the forest was secondary in origin and partly derived from a *Calophyllum* plantation. Others, especially oceanic islands like Mauritius, are highly susceptible. Baker (1877) noted that St. Helena was highly invaded even in the mid 1800s, and Vaughan (1937) records 139 species in Mauritius that had become naturalized subsequent to Baker's flora. The Hawaiian Islands, too, are plagued by many invasive exotics. For example, St. John (1973) lists 326 adventives in Hawaii, including two that also occur in Mauritius, *Psidium cattleianum* and *Rubus moluccanus,* whereas Tagawa (1979) lists the 110 most invasive species and stresses the seriousness of the problem in Hawaii. Rodrigues and Réunion, the other two Mascarene Islands, have also been extensively invaded by many of the same exotics that occur in Mauritius (Wiéhe, 1949; Cadet, 1977).

In Mauritius, Vaughan & Wiéhe (1937, 1941) stated that invasion by exotic plants was already becoming a serious problem by the 1930s and that their spread was probably accelerated by introduced exotic bulbuls and animals such as pigs and the crab-eating macaque. Although they omitted exotics from their survey at Macabé, Vaughan & Wiéhe (1941) noted that it was "... impossible to find even a small area free from exotics, and there is no forest into which the ubiquitous *Ardisia* . . . and *Psidium* . . . have not penetrated." At Macabé they recorded ca. 16,000 indigenous seedlings and plants less than 1 cm diam. and 50 cm tall per hectare.

They also studied regeneration in several disturbed forests. In a "pole forest" where selective felling of native species had been carried out for about 20 years and invasion by *Psidium, Ardisia,* and *Rubus* had taken place, they found 148 *Ardisia,* 49 *Psidium,* and 16 indigenous seedlings in a 1 m^2 plot. In another thicket of secondary origin composed largely of *Psidium* with a few indigenous remnants and an understory of *Ardisia,* the ground stratum consisted of numerous *Psidium* and *Ardisia* seedlings, but no native species were present. They noted that *Ligustrum,* introduced in 1904, had not yet spread to their study area at Macabé but was highly invasive elsewhere; there is virtually no part of the upland plateau now free from it. They suggested that succession in upland secondary thickets would normally lead to dominance by *Litsea monopetala* but that succession in some cases could be arrested by *Rubus moluccanus.*

Data from our seedling plots at Brise Fer and from Lorence & Sussman (1986) show that even in the absence of cutting and disturbance invasion is a serious problem in the upland forest (Table 6; Lorence & Sussman, 1986). Of the 34 species less than 2.5 cm diam. present in the plots (excluding those not identified to family), 27 (79.4%) were indigenous and only seven (20.6%) exotic. Of the 3,871 total seedlings and juveniles present, however, only 100 (2.6%) were indigenous as opposed to 3,771 (97.4%) exotics! Indeed, ripe fruits of the exotics litter the forest floor at certain times of the year (Fig. 3B). Of the exotic seedlings, 2,789 (72.4%) were privet, 842 (21.9%) were *Ardisia,* 97 (2.5%) were *Psidium,* 15 (0.39%) were *Litsea,* 5 (0.13%) were *Hiptage,* and 1 (0.03%) was *Ravenala. Rubus moluccanus,* an edge and gap species now present in great abundance at Macabé, was not recorded in our plots but occurs along clearings (Fig. 3A) and may be expected at a later stage of forest degradation.

TABLE 6. Summary of seedling plot data at Brise Fer. Total indigenous families (excluding 2 individuals not determined to family), 14; total exotic families, 7. Habit of indigenous species: 23 trees, 2 vines. Habit of exotic species: 4 trees, 2 shrubs, 1 vine.

Status	Number of Species	% Total	Number of Individuals	% Total
Indigenous	27	79.4	100	2.6
Exotic	7	20.6	3,771	97.4
Total	34	100.0	3,871	100.0

None of the indigenous species alone accounted for even 1% of the total, and only six amounted to above 0.1% of the total: *Psathura* (14 individuals), *Memecylon* (two species with 12 individuals), *Nuxia* and *Monimiastrum* (7 each), and *Allophyllus* (5). The remaining 21 indigenous species all had low numbers, below 0.1% of the total. Particularly striking is the fact that of the nine canopy species, only three showed any signs of regeneration: *Nuxia* (17 individuals, 0.18% total), *Elaeodendron* (2 individuals, 0.05%), and *Diospyros,* the most abundant canopy species, had only one (0.03%).

Most of the indigenous second stratum species also showed low rates of regeneration. Notably, the most abundant native species, *Erythrospermum monticolum* var. *pyrifolium,* had but a single seedling, and *Tabernaemontana,* the second most abundant in this stratum, had none. Second stratum species with relatively higher regeneration rates were: *Monimiastrum* (highest, with 7 individuals), *Memecylon* (two species, 12 individuals) (Fig. 3D), and *Allophyllus* (5). The remaining species were either represented by only one or two seedlings or no regeneration at all was recorded. The highest number of native seedlings belonged to the understory treelet *Psathura* (14), whereas among the lianas juveniles were recorded only for *Hugonia* (2) (Fig. 2D). This disparity in regeneration rates between exotic and native species helps explain why Macabé forest is dying. Our data for Brise Fer, perhaps suggestive of what Macabé was like some 50 years ago, indicates that the same invasion is occurring here that is apparent elsewhere in Mauritius native upland forests, even without direct human intervention.

What will be the future of the upland wet for-

ests of Mauritius? We anticipate that they will follow the same pattern as Macabé, gradually being replaced by dense thickets of exotics, especially privet, guava and *Ossaea marginata*. In spite of being one of the most recently introduced exotics (Table 1), privet has by far the most seedlings at Brise Fer (72.42%), and personal observations show it to be the most vigorous and invasive species in the Mauritian uplands, where it frequently forms dense, impenetrable thickets to the exclusion of virtually all other species. It is interesting that another adventive privet species (*Ligustrum lucidum*) has completely taken over the southern extreme of neotropical forest in northern Argentina (E. Zardini, pers. comm.). *Ardisia*, second with 21.9% of the seedlings, and guava, third with 2.5%, are both more shade tolerant than privet. Potentially much more competitive is the wiry shrub *Ossaea marginata* which, although still scarce at Brise Fer, forms dense stands in the lower stratum in parts of Mt. Cocotte and Macabé that choke out most other plants. *Litsea*, a medium-sized tree, is not very abundant (0.39% total) and does not appear to represent much of a threat here. The vine *Hiptage* is scarce and only marginally successful at Brise Fer, preferring the drier conditions along the western escarpments of the central plateau where it twines around and eventually strangles trees. *Ravenala*, on the other hand, prefers much wetter or even marshy ground where it is capable of forming dense forests, for example on Mare Longue Plateau and in the eastern mountain ranges.

In general, valley bottoms heavily shaded by large trees were found to have fewer seedlings, both native and exotic, although *Ardisia* was more abundant there. More seedlings were found on steep slopes and hillsides where the trees were shorter and the shading less, especially on crests. Here tremendous densities of privet seedlings were encountered, but little *Ardisia*. The same was true for tree falls and along forest margins (Fig. 3A). Although it is difficult to generalize, the definite patchiness noted in the distribution and density of seedlings of the three most common exotics suggests that forests in more protected areas such as valleys are denser and will resist the exotic onslaught for a longer time. Certainly cyclone damage, such as occurred at Macabé in 1960 (Vaughan, 1968), and human disturbance can enable exotics to gain an immediate foothold, thus accelerating invasion.

What can be done to save the native forests? Control of the exotic animals that disperse their seeds might be suggested. Although personal observations suggest that seeds of the three major exotics encountered in this study can germinate readily without passage through any animal vector, birds undoubtedly play a significant role in dispersing them. Mammals such as crab-eating macaques eat guava fruits and therefore probably also accelerate their spread. It is also probable that they are to some degree responsible for inhibiting regeneration of certain native species by eating flowers and unripe fruits (Owadally, 1980; Sussman & Tattersall, 1981). However, population density of the macaques is very low in the less invaded areas of mature native forest, and preliminary research (Sussman & Tattersall, 1986) suggests that the spread of the monkey population may actually follow the invasion of exotic plants rather than precede it. In addition, it is apparent that browsing activity by deer and rooting by pigs in areas with dense populations of these animals have a significant impact on indigenous regeneration in the native forest understory (Owadally, 1980). Finally, it is possible that allelopathic substances from the leaves of the exotics may play a role in inhibiting germination of indigenous species, an aspect which should be investigated.

It is obvious that stringent weeding programs such as that currently being carried out by the Forestry Department at tiny Perrier Reserve (ca. 1.5 ha) could save the upland forests of Mauritius. Here complete removal of competing exotics has enabled the indigenous species to regenerate prolifically (pers. obs.). However, as weeding on a large scale is both logistically and economically untenable for the much larger remaining nature reserves and Crown Lands, biological control is probably the only feasible alternative. Such a campaign was successfully carried out in Mauritius against the exotic *Cordia macrostachya* (Jacq.) Roem. & Schult., a weed of *Furcraea* fiber plantations (Williams, 1960), although ironically *Furcraea foetida* Haw. itself has now become a serious weed in the drier parts of the island. Also, biological control with insects and pathogens has been effective in controlling certain weeds in the Hawaiian Islands (Tagawa, 1979). Clearly, unless something can be done to stem the invasion of the remnants of native Mauritian forest by exotic species, the Mauritian endemics will be doomed to extinction.

Conclusions

The Mauritian flora evolved gradually over nearly eight million years as new elements were slowly added by immigration from distant source areas, the nearest being Madagascar, some 920 km to the west. The relaxation from competition by new arrivals allowed the evolution of highly specialized forms as has occurred on many such isolated oceanic islands (Carlquist, 1974). Slow growth and low germination rates were not strongly selected against, as the arboreal species evolved hard wood, sclerophyllous leaves, and dense, interlocking canopies to resist cyclonic onslaughts. With the arrival of man a plethora of new plant and animal species with which the native species had to contend was introduced within the space of a few centuries. Many of these exotic plants, like privet and guava, have the competitive advantage of rapid germination and growth rates in addition to being preadapted to existing pollinators and dispersal vectors. As a result, many of the indigenous species are now being outcompeted to extinction. No doubt herein lies the unfortunate destiny and ultimate demise of all too many island floras unless man chooses to intervene and save them.

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THE RELATIONSHIPS AND AFFINITIES OF THE MADAGASCAN *ANTHOSPERMUM* SPECIES (RUBIACEAE)[1]

CHRISTIAN PUFF[2]

ABSTRACT

The Madagascan species of *Anthospermum* (eight; all endemic) show the following relationships and affinities: (1) Madagascan species related both with each other and with a widely and disjunctly distributed, essentially afromontane species group; (2) a Madagascan species closely allied to a south central and southeast African species pair but without close relatives in Madagascar; (3) a Madagascan species pair without allies in Madagascar but presumably remotely allied to a widely distributed African species; (4) a vicarious species pair without obvious affinities to either Madagascan or African mainland species. The position of *Anthospermum* within the tribe Anthospermeae and the origin of the Madagascan species is briefly discussed.

RÉSUMÉ

Les espèces malgaches d'*Anthospermum* (huit, toutes endémiques) montrent les relations et affinités suivantes: (1) espèces malgaches reliées les unes aux autres et avec un groupe d'espèces essentiellement afromontanes avec une distribution répandue et disjointe; (2) une espèce malgache étroitement liée à deux espèces du centre-sud et du sud-est de l'Afrique mais sans parent proche à Madagascar; (3) deux espèces malgaches sans parent proche à Madagascar mais vraisemblablement vaguement reliées à une espèce africaine que l'on trouve sur une grande étendue; (4) deux espèces sans affinités manifestes avec des espèces malgaches ou du continent africain. La position d'*Anthospermum* dans la tribu des Anthospermées et l'origine des espèces malgaches sont brièvement mentionnées dans cette présentation.

The tribe Anthospermeae (Rubiaceae) is represented in Africa and Madagascar by the subtribe Anthosperminae. It comprises the genera *Anthospermum* (widely distributed), *Nenax* (South Africa and Namibia), *Galopina* (southeastern Africa), and *Carpacoce* (Cape Floristic Region). The genus *Phyllis* is endemic to the Canary Islands and Madeira.

The Anthospermeae are, except for the genus *Theligonum* (Theligoneae), the only (secondarily) wind-pollinated members of the Rubiaceae. As anemophiles they are characterized by a set of features which are otherwise unusual or absent in the family—a wide array of different sex forms in individual plants; morphological-anatomical adaptations such as increased receptive (i.e., stigma) surfaces; development of secondary sex characters in dioecious taxa; etc. (Puff, 1982). The Anthosperminae are thus a most rewarding group for a detailed study. In the subtribe, *Anthospermum* is the largest and most widely distributed genus (Africa south of the Sahara and Madagascar, Fig. 1; *A. herbaceum* also extends into southwestern Arabia). *Anthospermum* comprises 39 species (49 taxa). The highest concentration of taxa is found in southern Africa: 21 species (29 taxa; 54% and 59%, respectively) occur in the *Flora of Southern Africa* area, of which 18 species (26 taxa; 46% and 53%, respectively) are endemic; of these, ten species (16 taxa; 25.5% and 32.5%, respectively) are endemic (or nearly so) to the southwestern Cape Floristic Region.

Madagascar has eight species (nine formally recognized taxa; i.e., 20.5% and 18% of the species and taxa, respectively), all of which are endemic. Without exception, they occur in the "Région du vent" or "Région orientale" (cf. Perrier de la Bâthie, 1936; Humbert, 1955, 1965; Rauh, 1973; "Eastern Malagasy Region": Koechlin, 1972). The species are confined to medium to high altitudes [(600–)800–2,600 m] and are mostly found in the Central Plateau area (associated with evergreen montane forests or forest remnants in the high mountains or on the western slopes of the Central Plateau in dry, evergreen sclerophyllous forest or remnants thereof).

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FIGURE 1. Distribution of the genus *Anthospermum* (shaded); *A. herbaceum* (black lines), *A. palustre* (dots), and *A. thymoides* (triangles).

THE SPECIES GROUPS

The Madagascan species of *Anthospermum* can be divided into three groups.

GROUP 1. Single- (to few-)stemmed, ± erect, to ca. 2 m tall, dioecious shrubs (*A. emirnense* Baker, *A. madagascariense* Hom. ex Puff, *A. isaloense* Hom. ex Puff).

Anthospermum emirnense is a quite widely distributed shrub, occurring from the Tampoketsa d'Analampitso and Lake Alaotra, south to the mountains around Fort-Dauphin; there is a

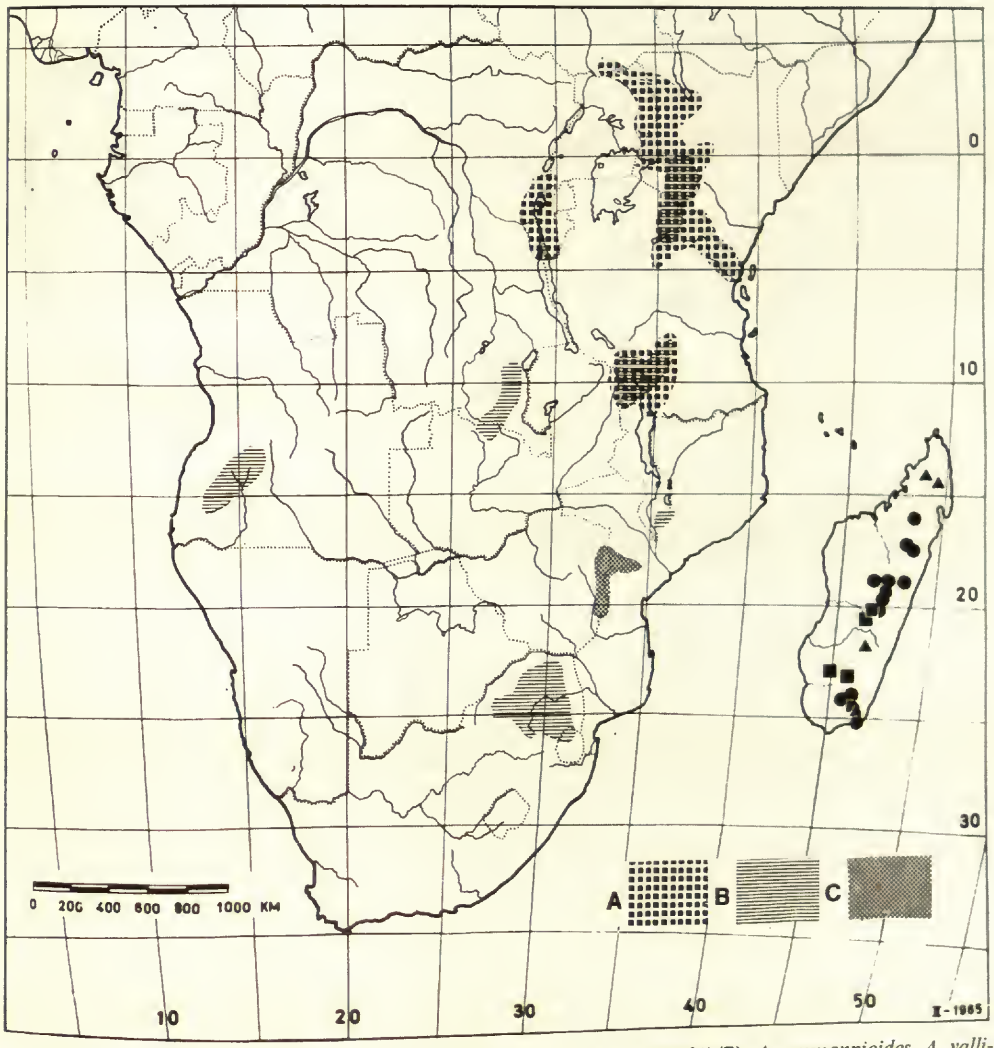

FIGURE 2. Distribution of *Anthospermum usambarense* (A); *A. welwitschii* (B); *A. ammannioides, A. vallicolum,* and *A. zimbabwense* (C); *A. emirnense* (dots); *A. madagascariense* (triangles); and *A. isaloense* (squares).

marked gap in distribution between the central Madagascan and the southern localities (not recorded from the Andringitra Massif!) (Fig. 2). The species occurs over a wide range of altitudes (800–1,700 m) and grows at the edge of montane forest as well as in remnants of dry, sclerophyllous forest (*Uapaca bojeri*–Chlaenaceae forest; "Tapia").

Anthospermum emirnense is very variable primarily in size, shape, and arrangement of leaves (decussate and/or in whorls of three, even within populations), and in internode lengths. Narrow- and small-leaved forms may, in habit, closely approach plants of the allied *A. madagascariense.*

Anthospermum madagascariense, confined to the high mountains of the island (ca. 1,800–2,600 m), mostly occurs in ericaceous scrub and is characterized by a markedly disjunct distribution range (Tsaratanana and Marojejy Massifs–Andringitra Massif–Andohahelo Massif) (Fig. 2). It is distinguished from the allied *A. emirnense* mainly by its narrower, usually more crowded leaves; by the conspicuous, persistent calyx lobes on the fruits (Fig. 3E); and by its hardly congested female inflorescences. The two speices are not sympatric and normally occur at different altitudes.

Anthospermum madagascariense is quite variable (leaf size, shape and arrangement; degree of

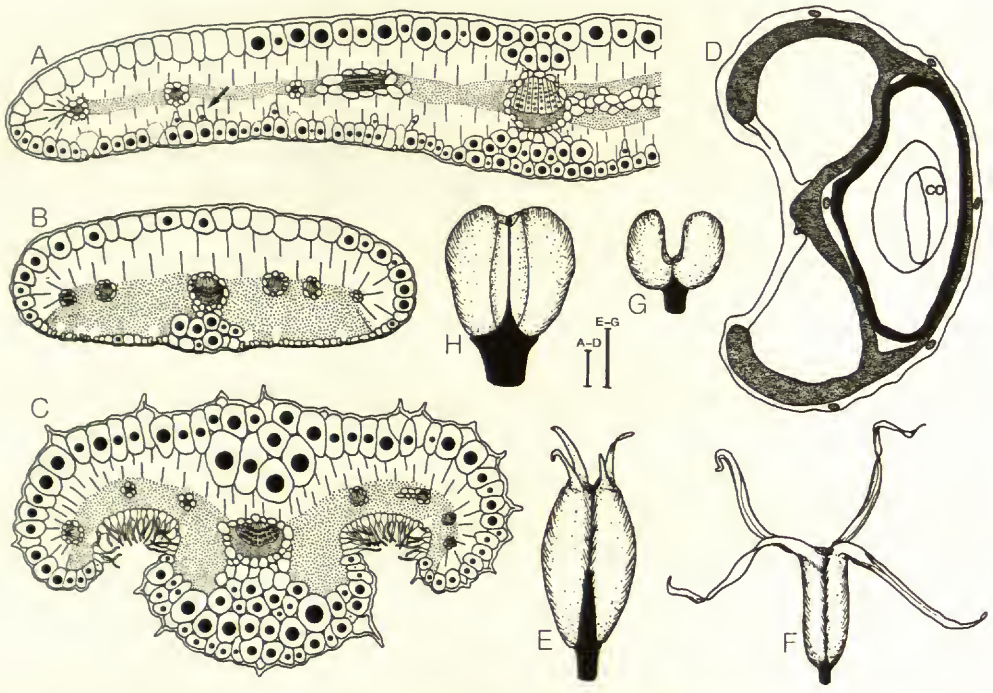

FIGURE 3. A–C. Leaf sections of *Anthospermum*.—A. *A. isaloense* (arrow indicates conelike cells; see text; *Puff 800814-3/2*).—B. *A. ibityense* (*Puff 800730-1/2*).—C. *A. longisepalum* (*Puff 800814-2/1*).—D. Mericarp section of *A. palustre* (*Perrier 3809*).—E–H. Fruits with carpophores and pedicels (black) in side view.—E. *A. madagascariense* (*Perrier 14428*).—F. *A. ibityense* (*Puff 800730-1/2*).—G. *A. thymoides* subsp. *thymoides* (*Perrier 14426*).—H. *A. herbaceum* (*Puff 810916-3/1*; Ethiopia).—A–C. Black dots = cells filled with tannins; chlorenchyma-palisade layers shown as straight lines; spongy mesophyll dotted.—D, E. Indumentum not drawn.—D. Endocarp dotted; seed-testa black, co-cotyledon. Scale 0.1 mm (A—D) and 1 mm (E—H), respectively.

crowding of the leaves). There are, however, some additional collections which no longer fully match the "typcial" *A. madagascariense,* even if the variability of the species is taken into consideration. *Humbert 6304* (P) from the Beampingaratra Massif (south), collected at a lower altitude than usual for *A. madagascariense* ("800–1,500 m"), has fruits which are densely covered with rather longer whitish, spreading hairs and crowned by four long, linear-lanceolate calyx lobes (labeled "var. *australe*" by Mme. A. M. Homolle on the herbarium sheet). *Perrier de la Bâthie 3807* (P) from the Manangarivo Massif (north, 1,400 m) has very shortly hairy to papillate fruits, crowned by broad calyx lobes and ± united in pairs ("var. *humile*" sensu A. M. Homolle). *Perrier de la Bâthie 3492* (P) from the Andringitra Massif (2,000 m) has fruits identical to the above-mentioned collection, but the corollas are ± hairy on the outside and the internodes are rather long (plants not densely leafy). The only available collection, moreover, has hermaphrodite and female flowers, whereas *A. madagascariense* plants are unisexual; too much emphasis should not be placed on this, however, as only one herbarium sheet is available. According to greenhouse observations on the allied *A. emirnense,* odd hermaphrodite flowers may occasionally occur on essentially unisexual plants ("*A. andringitrense*" sensu A. M. Homolle).

Thus in the north, in the south central area, and in the south, i.e., in all the areas where the "typical" *Anthospermum madagascariense* also occurs, there appear to be "forms" (in the sense of populations or races) which may be in the process of active evolution and "on their way" to becoming new species.

Both of the above species are clearly allied to the essentially afromontane *Anthospermum usambarense* group. This is represented in Africa by the East African *A. usambarense* K. Schum., the very widely and disjunctly distributed *A. wel-*

witschii Hiern, and three species (*A. ammannioides* S. Moore, *A. vallicola* S. Moore, and *A. zimbabwense* Puff) confined to the highlands of East Zimbabwe, neighboring parts of Mozambique, and Gorongosa Mt. (the first two) (Fig. 2). Some southeastern African species (e.g., *A. galpinii* Schltr. and the allied *A. littoreum* L. Bolus) also show certain affinities to this group; they are, however, not mapped here.

Anthospermum emirnense agrees with *A. ammannioides* in more characters than with any other species of that group (dimorphic inflorescences, i.e., congested, cylindrical female inflorescences; fruits without distinct calyx lobes; prevalence of ternately arranged leaves; etc.). Similar agreements in character states exist between *A. madagascariense* and *A. vallicola.* Nevertheless, similarities between the two above species pairs do not necessarily indicate a direct, close relation between them. It seems more likely that the entire *A. usambarense* group is a natural entity, derived from a common (possibly tropical African) ancestral stock. *Anthospermum ammannioides* established itself in the highlands of eastern Zimbabwe (where it ± "replaces" the widely distributed *A. welwitschii,* which has its nearest localities on Mt. Mlanje in the north and in the Transvaal in the south), and *A. emirnense* independently established itself on Madagascar and acquired a similar set of characters. The same may hold true for *A. vallicola* and *A. madagascariense.* The former evolved in the mountains of eastern Zimbabwe, the latter in the Madagascan mountains. Again, convergent evolution may account for certain morphological similarities such as leaf shape and size, or the conspicuous, persistent calyx lobes. *A. zimbabwense,* the third species confined to the highlands of eastern Zimbabwe, appears to be an offshoot of the tropical east African *A. usambarense,* which established itself in fire-prone grassland habitats.

Anthospermum isaloense can, with some reservations, probably also be associated with the *A. usambarense* group. It differs in various morphological characters (very reduced inflorescences; leaves), and an unusual and, in *Anthospermum,* unique leaf-anatomical feature of peculiar, ± conelike cells filled with a dark substance associated with the lower epidermis (Fig. 3A). The chlorenchyma structure of *A. isaloense,* with upper and lower palisade layers and a central spongy mesophyll, is, however, also found in some other taxa (Puff, 1986). Also, *A. isaloense* deviates from the above species in wood anatomy, as it does not have the "typical" rubiaceous wood type (primary woodiness) characteristic of the investigated taxa of the *A. usambarense* group (Koek-Noorman & Puff, 1983). *Anthospermum isaloense* is, moreover, typically found in (remnants of) *Uapaca bojeri*–Chlaenaceae–*Asteropeia* forest and rarely extends to higher altitudes. It occasionally grows in the same area as *A. emirnense* but has its main distribution in south central Madagascar and in the southern part of the island.

GROUP 2. Several- to many-stemmed, ± rounded to erect, to ca. 40(50) cm tall dwarf shrubs, which may be ♀, ♀, ♂, ♀ + ♀, seldom ♂ + ♀ + ♀ or ? ♀ + ♂ (*A. perrieri* Hom. ex Puff, *A. ibityense* Puff, *A. longisepalum* Hom. ex Puff).

Anthospermum perrieri, confined to central Madagascar, shows in its habit, characteristic, often reddish- to rusty-brown indumentum, stipular sheaths, and in floral morphology, a close and clear affinity to the species pair *A. whyteanum* Britten of south central Africa and *A. hispidulum* Sond. of South Africa and Swaziland (Fig. 4). Its hairy fruits are also similar but lack the distinct persistent calyx lobes typically present in the two African species. *Anthospermum perrieri* and *A. hispidulum* always have decussately arranged leaves, while *A. whyteanum* has a strictly ternate leaf arrangement.

Moreover, the three species grow in almost identical habitats (amongst rocks, in rock crevices, etc.). The Madagascan species has been recorded from granitic and gneissic areas. According to my field observations in Malawai and Zimbabwe, *Anthospermum whyteanum* is rather common on isolated granite hills and rocky outcrops; *A. hispidulum* often occurs over quartzite (Transvaal), sandstone (Natal), and also over granite.

On account of their unique set of characters, these three species occupy a somewhat isolated position within the genus; there are neither obvious, close allies on the African mainland nor in Madagascar.

Anthospermum ibityense and *A. longisepalum* are similar to the above only in their habit. Both species are characterized by mericarps with long, ± bandlike persistent calyx lobes (unique in the genus; Fig. 3F) and rather long, cylindrical corolla tubes. They are doubtlessly closely related but nevertheless differ in their indumentum (especially leaves and fruits densely covered with

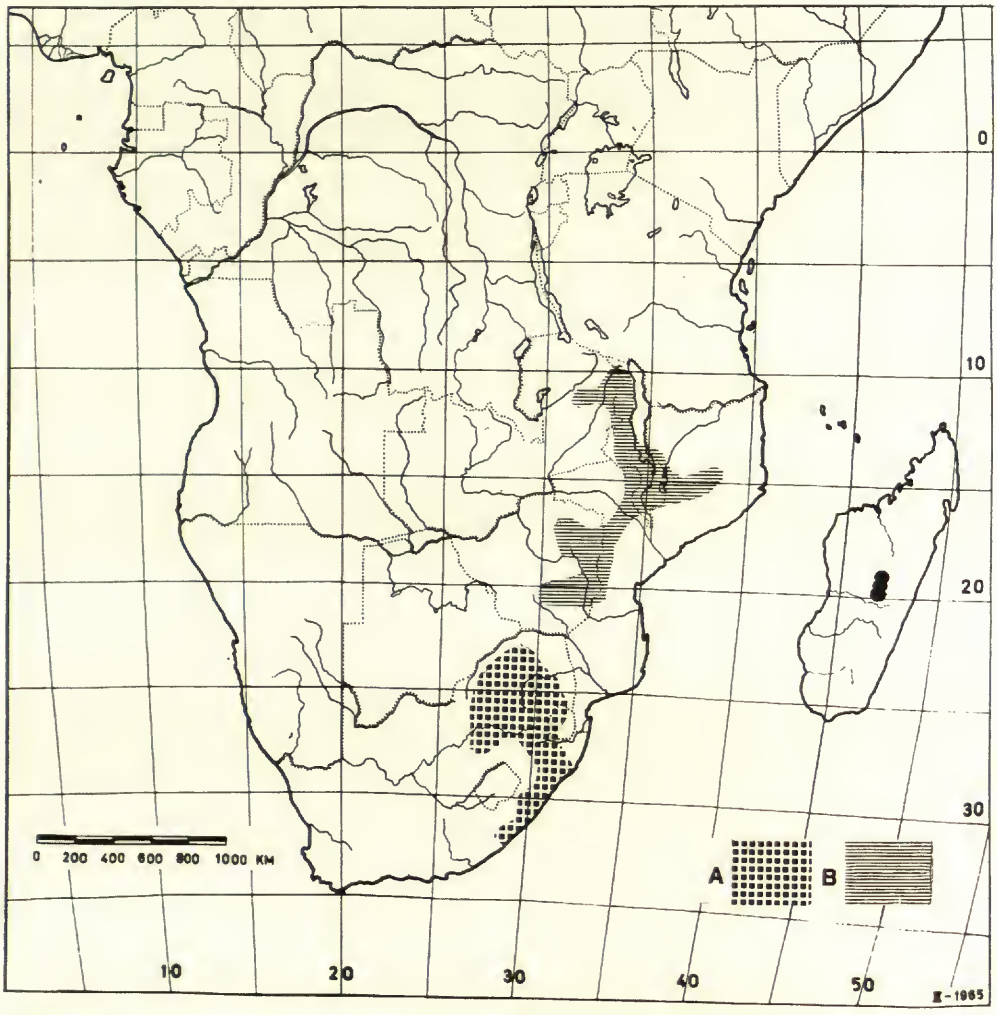

FIGURE 4. Distribution of *Anthospermum hispidulum* (A), *A. whyteanum* (B), and *A. perrieri* (dots).

papillae or very short hairs, *A. longisepalum*; glabrous, *A. ibityense*) and the length of the calyx lobes. Their leaf anatomy, furthermore, is strikingly different (compare Fig. 3B and 3C): the revolutely rolled leaves of *A. longisepalum* are unique in *Anthospermum* in that there is a hairy furrow on either side of the prominent midrib; the hairs are formed by epidermis cells (strongly xeromorphic!). *Anthospermum longisepalum* may have progressed to the total separation of the sexes (dioecy; further detailed field studies of populations, however, would be required to confirm this), while *A. ibityense* has ♀ or ♀ and perhaps also ♀ + ♀ and ♀ + ♂ plants.

Anthospermum ibityense has so far only been recorded from quartzite areas (Mt. Ibity) and *A. longisepalum* only from sandstone (Isalo). The two taxa can thus be considered a vicarious species pair.

Unusual features such as the long calyx lobes (adaptation to epizoochory?) and leaf anatomy in combination with rather primitive characters like the quite long, cylindrical corolla tubes account for the isolated position of this species pair. The pair has no apparent allies in either Madagascar or on the African mainland.

GROUP 3. Perennial herbs or subshrubs with stems to 60 cm long; the plants are ♀ or ♀ + ♀ (and also ♀?) (*Anthospermum palustre* Hom. ex

Puff; *A. thymoides* Baker subsp. *thymoides*, and subsp. *antsirabense* Puff).

Anthospermum palustre is only known from a few localities in central Madagascar. Information on herbarium sheets indicates that it is apparently confined to peat bogs ("tourbières"; see Straka, 1960, for details on such habitats in Madagascar). It is characterized by its herbaceous habit and flowers with long, ± cylindrical corolla tubes. The (scanty) available material has only ♀ flowers, but I am convinced that additional collections will, as in African taxa, also show other sex forms; the occurrence of at least ♀ + ♀ is predicted. (In Africa, certain species may have individual ♀ plants, but if populations are studied carefully, individuals with ♀ + ♀ flowers, strictly ♀ individuals and sometimes also ♂, ♀ + ♂ or even ♂ + ♀ + ♀ plants are also very likely to be found. Details on sex forms of individual plants and on sex distributions within populations and species will be discussed at great length in a future paper on African and Madagascan Anthospermeae.) The fruits are remarkable for two reasons. Firstly, *A. palustre* and the allied *A. thymoides* are the only species in the genus with fruits that have a very short commissure (i.e., the mericarps only touch each other in the lowermost part) (Fig. 3G). Secondly, the mericarps contain two air-filled pockets, formed by two armlike extensions of the sclerenchymtic endocarp, over which the thin exocarp is stretched (Fig. 3D). This second feature may have some dispersal-ecological importance in that these air-filled pockets may enable the mericarps to float.

Anthospermum thymoides is closely allied to the above. It has the same basic fruit structure but differs in the shape and warty indumentum of the mericarps (glabrous in *A. palustre*). The plants of *A. thymoides* are often slightly more woody at the base (and thus ± subshrubby) than *A. palustre*. On the basis of absence or presence of a characteristic indumentum of whitish, spreading hairs, two subspecies are distinguished, of which subsp. *thymoides* is quite widely distributed from around Antananarivo to the south of the island, whereas subsp. *antsirabense* has so far only been recorded from the surroundings of Antsirabe. *Anthospermum thymoides* is presumably no longer confined to wet habitats, although it has also been collected "at the edge of rice fields" and is found on dry rocky hills and in secondary vegetation (savoka) at altitudes of ca. 1,400–2,000 m.

The position of the species pair is not entirely clear. It certainly has no recognizable allies in Madagascar. Its affinities may lie with perennial herbs of the African mainland that, without exception, are, like *Anthospermum palustre* and *A. thymoides*, characterized by a rather "primitive" type of ♀ flower with a quite long and ± cylindrical corolla tube, as opposed to flowers with short, broadly funnel-shaped to subcampanulate corolla tubes. These species have quite complicated sex distributions (individual plants ♀, ♀ + ♀ . . . etc.; see *A. palustre*, above), although some obviously derived taxa amongst this group show a clear trend towards the total separation of the sexes (i.e., dioecy) at least at populational level. For reasons to be explained below, it is the very widely distributed, essentially afromontane *A. herbaceum* L. f. (Fig. 1) that perhaps shows a remote alliance to *A. palustre* and *A. thymoides*. Apart from its herbaceous habit and similar floral structure and sex distribution, its habitats seem to lend some support to a possible alliance. *Anthospermum herbaceum* typically occurs in moist to wet habitats, e.g., at the edge of streams, in dambos, etc. In southeastern Africa especially, considerable ecological radiation has taken place: in addition to "typical" plants, burnt grassland forms, trampled grassland forms, high altitude forms, sand-dune forms, etc. also occur (Puff, 1986). Its fruits (Fig. 3H), furthermore, show a faint morphological and anatomical resemblance to the two Madagascan species in question in that the two mericarps are separated by a ± broad vertical groove made up of sterile, exocarp tissue.

Discussion

The entire tribe Anthospermeae is very widely distributed, occurring mostly in subtropical and tropical regions of the Old and New World, and is largely confined to the southern hemisphere. It is subdivided into three well-defined subtribes, each of which has a clear-cut geographical range (Puff, 1982; Fig. 5). An analysis of the character states of all genera of the tribe indicates that the most primitive members are found amongst the subtribe Coprosminae, and especially in the genus *Coprosma*. This large genus has a wide, ± south-temperate, amphi-transpacific distribution (Van Steenis, 1962). The highest concentration of taxa is found in New Zealand (Oliver, 1935). Although it is difficult to establish the center of origin of *Coprosma* and, subsequently, also that of the Anthospermeae with any degree of certainty from the present-day distribution, I

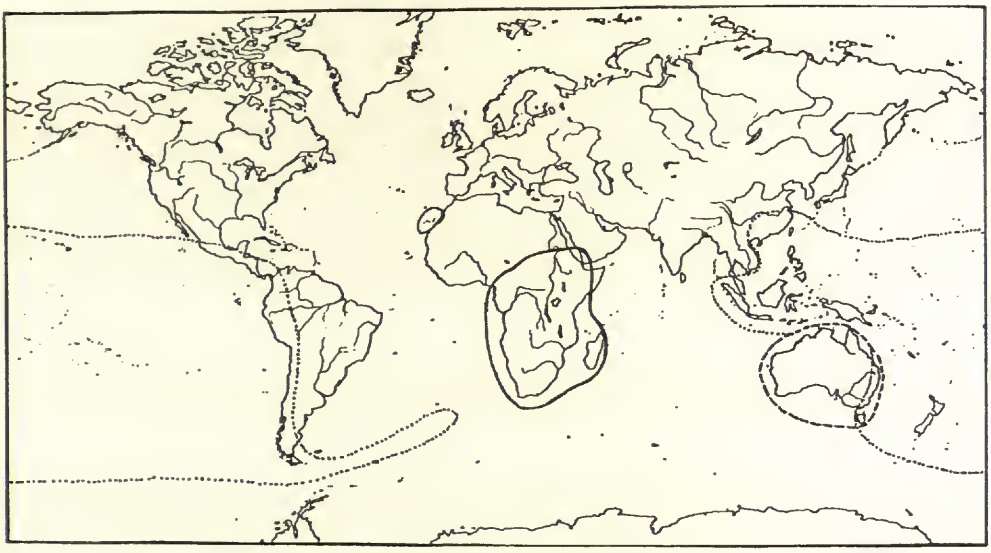

FIGURE 5. Distribution of the tribe Anthospermeae. Subtribe Anthosperminae, solid line; subtribe Coprosminae, dotted line; subtribe Opercullariinae, interrupted line.

assume for reasons to be discussed separately (Puff, 1986) that the tribe may have originated in the Australasian region. Various data, notably the occurrence of secondary anemophily in the entire tribe, seem to indicate that it did not originate in West Gondwanaland, which is thought to be the center of origin of many angiosperm orders (Raven & Axelrod, 1974). From there, the ancestral stock of the Anthospermeae could have spread, inter alia, to Africa, giving rise to the genera of the Anthosperminae.

On the basis of broad evidence to be published elsewhere (Puff, 1986), *Anthospermum* itself is likely to have originated in tropical Africa. Its ancestors were presumably forest-edge plants occurring in mountainous areas. If this is correct, it follows that the ancestral stock of *Anthospermum* could only have started to radiate from the Miocene onwards as East Africa was elevated and volcanos were built up along the rift zone (Axelrod & Raven, 1978). Thus *Anthospermum* is presumed to be a relatively young genus.

The data on the Madagascan taxa and their allies presented above indicate that the Madagascan species of *Anthospermum* were clearly not derived from a common (tropical?) African ancestral stock, arriving on the island at one particular point of time, but that different *Anthospermum* species groups or their ancestors reached Madagascar in successive "waves" at different times. The species in question, or their ancestors, must have reached Madagascar by long-distance dispersal because, notwithstanding the time of separation of the island from the African mainland, continuously favorable habitats for the relevant taxa are very unlikely to have existed at any time.

The herbaceous line of *Anthospermum,* represented in Africa by *A. herbaceum* and its allies, seems to have reached Madagascar relatively early. Thus its presumed Madagascan representatives, *A. palustre* and *A. thymoides,* had sufficient time to evolve their unique features. The shrubby (primarily woody) line of *Anthospermum,* represented by the *A. usambarense* group, may have established itself on the island in more recent times, as several character states of the mainland African and Madagascan taxa of this group are still similar to ± identical. The presumably rather derived (probably secondarily woody, cf. Koek-Noorman & Puff, 1983) and relatively young dwarf-shrubby line of *Anthospermum,* represented on the African mainland by *A. whyteanum* and *A. hispidulum,* is also likely to be a relatively recent newcomer to the island. As regards the allied, isolated and derived species pair, *A. ibityense* and *A. longisepalum,* it is difficult to make any speculations other than to assume that the ancestral stock from which it was derived may have reached Madagascar at a

relatively early stage. African mainland representatives of this stock may have become extinct.

It is also worth mentioning that none of the Madagascan taxa of *Anthospermum* show a clear and pronounced affinity to species or species groups confined to or centered in the Cape Floristic Region, the area of the highest concentration of taxa. Except for the isolated species pair *A. ibityense* and *A. longisepalum*, relationships exclusively lie with tropical (East) African taxa. This fits in with my ideas (Puff, 1986) that the southwestern Cape, as far as *Anthospermum* is concerned, is not the center of origin of the genus but is a secondary center of speciation. Finally, it should be pointed out that the African and Madagascan species of the genus *Galium* L. (Rubieae; Rubiaceae) have a basically very similar pattern of distribution and affinity as those of *Anthospermum* (Puff & Mantell, 1982), although in the former some of the species occurring in the mountainous areas of Madagascar and in the mountains of mainland Africa have not diverged as much, or are even still the same.

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THE ADAPTIVE ARRAY OF THE LEMURS OF MADAGASCAR

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ABSTRACT

There are 22 extant species of Malagasy lemur, and at least 14 species have become extinct within the last 2,000 years. The lemurs presently exist primarily in the coastal regions, where most of the remaining primary vegetation can still be found. Approximately half of the living forms are found in the eastern rainforest and half in the drier forests of the west. Furthermore, half of the species are active during the day, whereas half are nocturnal. In the wet forests of the east, as many as five diurnal and six to seven nocturnal species might be found to coexist in some regions. Only one of these has been the subject of long-term study and seven species of the eastern region have never been studied. In fact, the present distribution and status of many eastern species at this time are unknown. Our knowledge of the lemurs living in western Madagascar, especially in the southwest and west, is much better than of those of the east. Most of the western species have been the subject of at least preliminary research. In many forests of the southwest as many as five nocturnal and three diurnal species coexist. Although the five nocturnal species subsist on abundant and often similar resources in the wet season, their habitat preferences are quite distinct in the dry season when resources are scarce. Two of the species hibernate or enter into torpor, one feeds on insect secretions, one on gums, and one eats mainly leaves. The diurnal species have extremely different habitat preferences, both from the nocturnal forms and from each other, throughout the year. Although Madagascar offers a unique opportunity for the study of ancient ecological communities and the lemurs allow us an opportunity to study our earliest relatives, we as yet know very little about these life forms. What we do know, however, is intriguing and should encourage us to increase our research efforts and our efforts to conserve what remains of the natural flora and fauna of this remarkable island.

RÉSUMÉ

Il y a 22 espèces existantes de lémurs malgaches et au moins 14 espèces ont disparu durant ces 2,000 dernières années. Actuellement, les lémurs ne vivent que dans les régions côtières, là où se trouve la plupart de ce qu'il reste de la végétation primaire. Environ la moitié des formes vivantes se trouve dans les forêts humides de l'est et l'autre moitié dans les forêts plus sèches de l'ouest. De plus, la moitié des espèces est active pendant la journée tandis que l'autre moitié est nocturne. On peut trouver jusqu'à cinq espèces diurnes et six à sept espèces nocturnes qui cohabitent dans certaines régions des forêts humides de l'est. Une seule de ces espèces a été longuement étudiée et sept espèces de la région de l'est n'ont jamais été examinées. En fait, jusqu'à présent, on ne connait pas la répartition et le statut actuels de nombreuses espèces orientales. Les lémurs qui habitent dans la partie occidentale de Madagascar, surtout le sud-ouest et l'ouest, sont bien mieux connus que ceux de l'est. La plupart des espèces occidentales ont été l'objet d'études au moins préliminaires. Dans de nombreuses forêts du sud-ouest jusqu'à cinq espèces nocturnes cohabitent avec trois espèces diurnes. Bien que les cinq espèces nocturnes subsistent grâce à des ressources abondantes souvent similaires pendant la saison humide, elles préfèrent des habitats distincts pendant la saison sèche quand les ressources sont limitées. Deux des espèces hibernent ou s'engourdissent, une se nourrit de sécrétions d'insectes, la quatrième de gommes, et la dernière mange principalement des feuilles. Les espèces diurnes choisissent des habitats très différents qui varient selon les espèces et diffèrent de ceux des espèces nocturnes au cours de l'année. Madagascar offre une chance unique d'étudier les anciennes communautés écologiques, et les lémurs nous permettent d'étudier nos parents les plus anciens. Néanmoins, nous savons très peu de choses sur ces espèces jusqu'à présent. Ce que nous savons, cependant, est intéressant et devrait nous encourager à continuer nos recherches et à pourvuivre nos efforts pour conserver ce qu'il reste de la flore et de la faune naturelles de cette île remarquable.

Currently there are 22 species of lemur (Table 1) and at least 14 additional species have become extinct within the last 2,000 or so years. Lemurs are presently found principally in coastal regions where most of the remaining primary forest vegetation can still be found. Madagascar is divided into two major vegetation zones, the dry western or occidental zone and the wet eastern or oriental zone (Fig. 1). Most extant species of lemur are found in either the western forests or eastern forests, few are distributed in both vegetation zones. Nine species are found only in the east, nine only in the west, and four are found in both regions. Two of the latter (*Avahi laniger* and *Hapalemur griseus*) have extremely localized distributions in the west. Thus only two species (*Le-*

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TABLE 1. Lemur species of Madagascar, indicating geographical location (W = west, E = east, B = both vegetation zones); diurnal (D) or nocturnal (N) activity cycle; and extent of research conducted (0 = none, ST = short-term, LT = 6 or more months).

	Distribution			Activity		Research		
	W	E	B	D	N	0	ST	LT
Lemurinae								
Lemur catta	X			X				X
L. fulvus	X	X	**X	X				
L. macaco	X			X		X		X
L. mongoz	X				X		X	
L. coronatus	X			X			X	
L. rubriventer		X		X		X		
Varecia variagata		X		X		X		
Hapalemur griseus	*X	X	X	X			X	
H. simus		X		X		X		
Lepilemur mustelinus	X	X	**X		X			X
	7	6	3	8	2	4	3	3
Cheirogaleinae								
Cheirogaleus medius	X				X		X	
C. major		X			X	X		
Microcebus murinus	X				X		X	
M. rufus		X			X		X	
Mirza coquereli	X				X		X	
Allocebus trochotis		X			X	X		
Phaner furcifer	X	?	?		X		X	
	4	3	0	0	7	2	5	0
Indriidae								
Propithecus verreauxi	X			X				X
P. diadema		X		X		X		
Indri indri		X		X				X
Avahi laniger	*X	X	X		X	X		
	2	3	1	3	1	2	0	2
Daubentoniidae								
Daubentonia		X			X		X	
	0	1	0	0	1	0	1	0
Totals	13	13	2+2	11	11	8	9	5

* Western populations of these two species have a very limited and localized distribution.
** These species have a number of distinct subspecies. In fact *Lepilemur* has been divided into seven species by some authors.

mur fulvus and *Lepilemur mustelinus*) have island-wide distributions and these have a number of very distinct subspecies. Some authors believe that *Lepilemur* should include seven species (Petter et al., 1977).

Half of the Malagasy lemurs are diurnal (11 species) and half are nocturnal (11 species) (Table 1). The Cheirogaleinae and *Daubentonia* are nocturnal (eight species). *Lemur mongoz, Avahi laniger,* and possibly *Lepilemur mustelinus* are secondarily nocturnal, having most likely evolved from diurnal ancestors. Of the nocturnal forms five are found only in the east, four only in the west, and two in both zones. The diurnal lemurs are distributed as follows: four exclusively eastern, five western, and two are located on both sides of the island. No diurnal prosimian occurs outside of Madagascar or the Comoro Islands.

Thus, a quick overview of the major geographic distribution and activity cycles of the Lemuriformes gives two major adaptive groupings: the eastern/western split and the nocturnal/diurnal split. As one would expect, fewer species are able to coexist in the dry seasonal deciduous forests

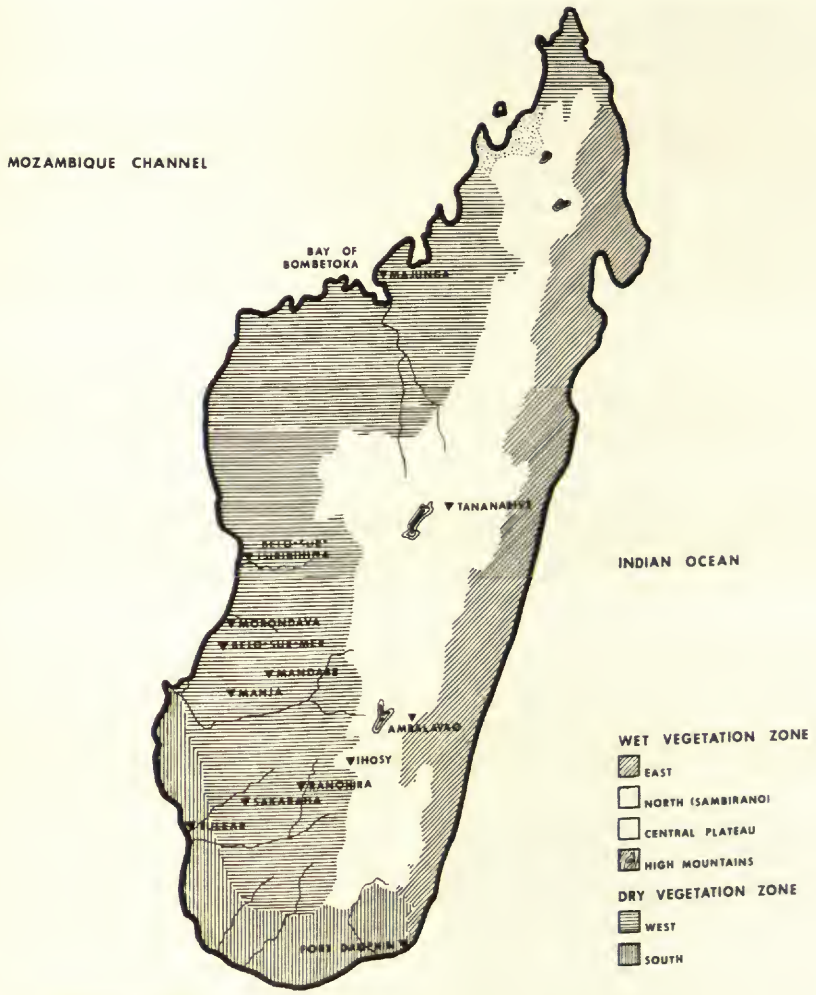

FIGURE 1. Vegetation zones of Madagascar.

and xerophytic forests of the west than in the evergreen rainforests of the east. In some eastern forests, as many as five diurnal and possibly six to seven nocturnal lemurs can coexist in the same forest (Table 2), whereas in the desertlike and riverine forests of the south usually only four or five species coexist. The west and northwest are wetter than the south and contain a mix of vegetation. These areas contain an intermediate number of coexisting lemurs. In each of these there may be three species of diurnal lemurs and five to six nocturnal forms. Three diurnal lemurs, *Lemur coronatus* and the two species of *Hapalemur*, have very specific habitat preferences and are not usually found in sympatry with other species.

Unfortunately, only one eastern rainforest lemur has been studied in any detail. Thus we know very little about the behavior or ecology of these species, nor of the habitat preferences of the coexisting forms. Only *Indri* has been the subject of long-term detailed research and *Daubentonia, Microcebus rufus,* and *Hapalemur griseus* have been studied for a short time. Little or nothing is known of free-ranging *Lemur rubriventer, Varecia variagata, Propithecus diadema, Avahi laniger, Cheirogaleus major, Allocebus trochotis, Hapalemur simus,* or of eastern populations of *Lemur fulvus* and *Lepilemur*. Long-term studies of the Lemuriformes in the eastern rainforest and their current distribution are a major priority at this time. Five of these lemurs may

TABLE 2. Species potentially coexisting in forests of various regions of Madagascar, and relative amount of research conducted on each (LT = long-term (6 months or over); ST = short-term, 0 = none).

Diurnal	Nocturnal
Eastern Forests	
Lemur fulvus (0)	*Lepilemur mustelinus* (0)
Lemur rubriventer (0)	*Cheirogaleus major* (0)
Varecia variagata (0)	*Microcebus rufus* (ST)
Propithecus diadema (0)	*Allocebus trochotis* (0)
Indri indri (LT)	*Avahi laniger* (0)
	Daubentonia madagascariensis (ST)
	Phaner furcifer (ST)?
Northwestern Forests	
Lemur fulvus (0)	*Lemur mongoz* (ST)
Lemur macaco (0)	*Lepilemur mustelinus* (0)
Propithecus verreauxi (LT)	*Cheirogaleus medius* (0)
	Microcebus murinus (0)
	Mirza coquereli (ST)
	Avahi laniger (0)
Southwestern and Western Forests	
Lemur fulvus (LT)	*Lepilemur mustelinus* (ST)
Lemur catta (LT)	*Cheirogaleus medius* (ST)
Propithecus verreauxi (LT)	*Microcebus murinus* (ST)
	Mirza coquereli (ST)
	Phaner furcifer (ST)
Southern Forests	
Lemur catta (LT)	*Lepilemur mustelinus* (ST)
Propithecus verreauxi (LT)	*Microcebus murinus* (ST)
	Cheirogaleus medius (ST)

be extremely rare over most of their range, and their current status must be determined. *Allocebus* is only known from one sighting in the wild and may well be extinct, and *Daubentonia* is in jeopardy throughout its range. *Lemur ribriventer, P. diadema,* and *H. simus* are also probably in eminent danger of extinction.

Studies of western populations of lemurs have been more frequent and the ecological interactions between coexisting populations of many of these forms are reasonably known. Preliminary quantitative studies have been made on all nocturnal species of the western zone except *Avahi.* Detailed studies of *Lemur catta, L. fulvus,* and *Propithecus verreauxi* have been conducted in the south and southwest of the island. Thus, we have a good idea of the behavior and ecology of these species and their habitat preferences. We also have an idea of how they partition their resources and are able to coexist sympatrically in some portions of their range. In the rest of this paper, I will review the literature on eight western sympatric species (five nocturnal and three diurnal) in order to illustrate some of their basic ecological adaptations.

Nocturnal Lemuriformes of Western Madagascar

A preliminary study of five nocturnal Malagasy prosimians has been carried out in a highly seasonal forest, Marosalaza, in western Madagascar: *Cheirogaleus medius, Microcebus murinus, Mirza coquereli, Phaner furcifer,* and *Lepilemur mustelinus* (Petter, 1978; Hladik et al., 1980). Simultaneous studies were conducted on the same species under simulated climatic conditions by a team from the Centre National de la Recherche Scientifique in Brunoy, France (Charles-Dominique et al., 1980). Research at the same and other sites in Madagascar has focused on four of the same species: *M. murinus* (Martin, 1972, 1973); *M. coquereli* (Petter et al., 1971; Andrianarivo, 1981); *P. furcifer* (Petter et al., 1971, 1975); and *L. mustelinus* (Charles-Dominique & Hladik, 1971; Russell, 1977).

In a detailed study of the climate and vegetation, Hladik (1980) found that the Marosalaza forest is extremely seasonal in production of flowers, fruit, and leaves. The dry season, with little productivity of these items, occurs in the austral winter between April/May and September (Fig. 2). Insect availability is also seasonal, following the pattern of leaf production. This seasonality is correlated with specific dietary and physiological adaptations of the five small nocturnal prosimians.

The most extreme adaptation to the seasonal production of the forest is found in *Cheirogaleus medius* (the fat-tailed dwarf lemur). Unlike any other primate, *C. medius* actually hibernates for 6–8 months during the year. It emerges in November before the rainy season when food production is at a maximum. During hibernation three to five individuals may sleep together in deep hollows of tree trunks. During the active period, the animals accumulate large fat reserves under the skin and inside the tail (Fig. 3) and can gain over 50% of their body weight, from 142 to 217 g.

Cheirogaleus medius is quadrupedal and not

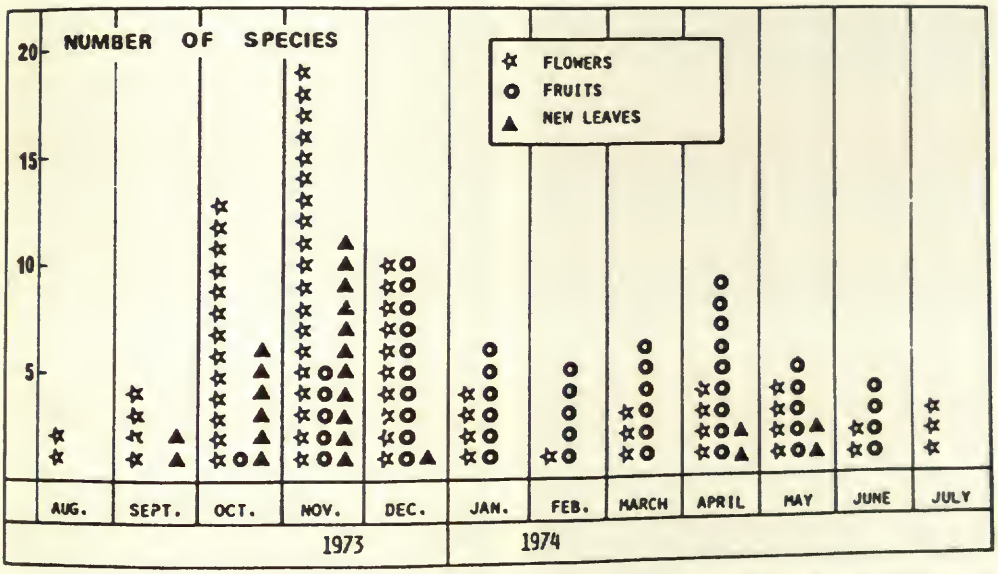

FIGURE 2. Food availability throughout the year at Marosalaza forest. Symbols indicate number of species producing potential foods in a 2,200 m^2 sample. (Adapted from Hladik et al., 1980.)

as quick-moving nor as agile as species of *Microcebus* or *Phaner furcifer* (Petter et al., 1977). The tail, when thickened, prevents acrobatic locomotion. The fat-tailed lemur is active mainly 2–9 m in height and uses medium-sized supports. In general, *C. medius* is considered an opportunistic frugivore. The seasonal variation in diet follows food availability: nectar and fruit in November/December; fruits and an increasing proportion of insects (though never more than 10%) from December to January; and a higher proportion of fruits at the time of fattening, preceding hibernation (Hladik et al., 1980). These patterns of food intake seem to be mirrored in captive *C. medius* given a choice of foods (Petter-Rousseaux & Hladik, 1980).

Microcebus murinus (the lesser mouse lemur) does not hibernate but has a period of lethargy during the dry season in Marosalaza. At this time, the animals may stay in hollow trunks for several consecutive days, and overall activity is considerably reduced. As with *Cheirogalus medius,* fat is stored under the skin in the tail, but these changes are not as great and tail fattening is not as spectacular in *M. murinus.* Russell (1975) found that in *M. murinus* some individuals are lethargic and have depressed body temperatures, while others are active. This may be true in the Marosalaza forest, since some lesser mouse lemurs are observable throughout the year. In a study in a warmer, less seasonal, littoral rainforest in southern Madagascar, Martin (1972) did not observe a period of lethargy in his study population.

The lesser mouse lemur (Fig. 4) is about the

FIGURE 3. *Cheirogaleus medius* with a fattened tail. (Photo by J. J. Petter.)

FIGURE 4. The lesser mouse lemur (*Microcebus murinus*), the smallest living primate. (Photo by Benjamin Z. Freed.)

FIGURE 5. Coquerel's mouse lemur (*Mirza coquereli*). (Photo by Benjamin Z. Freed.)

size of a mouse (60–150 g). In locomotion, it generally scurries like a mouse but can grip fine terminal branches of bushes and trees and can leap distances over 3 m (Martin, 1972). The lesser mouse lemur usually lives in areas with dense foliage and fine terminal supports and is active at all heights in the forest where suitable vegetation occurs, but most of its activity takes place low in the forest. *Microcebus murinus* descends to the ground to hunt insects and cross short open areas. The diet of *M. murinus* consists mainly of insects and fruit. However, even though the lesser mouse lemur is the smallest primate, less than half of its diet is made up of insects (Martin, 1972; Hladik et al., 1980). Besides fruit, it feeds on small amounts of gum, leaves, and nectar.

Just as in *Cheirogaleus medius, Microcebus murinus* studied in captivity showed a variation in propensity for different dietary components at different periods of the year. Seasonal variations in dietary choice, body weight, body temperature, basal metabolism, and water intake (Perret, 1979) seem to be related to physiologically based endogenous rhythms that enable these two diminutive species to live in forests with highly seasonal climates and productivity.

Mirza coquereli (Fig. 5) is found in the most dense part of the forest (Pages, 1980). In Marosalaza, Coquerel's mouse lemur seems to be as insectivorous as *Microcebus murinus* and also eats large amounts of fruit. However, in the beginning of austral winter, 50% of the observed feeding of *M. coquereli* is on the secretions of homopteran insects, mainly colonial aggregates of *Flatida coccinea* (Pages, 1980). At the larval stage, these insects exude a sweet secretion when disturbed. *Mirza coquereli* regularly visits several colonies each night, licking the liquid when deposited. These secretions have an extremely low protein content, and insects and small vertebrates provide the major source of protein for Coquerel's mouse lemur. Hladik et al. (1980) claim that its peculiar ability to exploit the secretions of insects, which are available during both wet and dry months, enables this species to be active throughout the year.

Phaner furcifer (Fig. 6) is about the same body size as *Murza coquereli* (440 g) and also shows no seasonal changes in body weight nor in basal

FIGURE 6. *Phaner furcifer.* (Photo by the author.)

metabolism (Petter, 1978; Hladik et al., 1980). *Phaner furcifer* is highly specialized to feed on gums and exists mainly on this resource, which is available throughout the year. It is a very quick-moving, agile, quadrupedal animal which spends most of its time on the horizontal branches of the canopy, 3–4 m in height. However, *P. furcifer* also ranges through the various vertical strata of the forest, from the ground to above 10 m (Petter et al., 1971, 1975). *Phaner* possesses keeled, pointed nails, allowing it to climb up large vertical tree trunks and facilitating gum feeding on large branches.

The greatest proportion of the diet is made up of gums from *Terminalia* species. The gums are produced to seal wounds caused when coleopteran larvae burrow tunnels in the bark. Other species of tree are visited less frequently for gums and, especially during the wet season, for floral nectar and fruit. *Phaner* has been observed for long periods clinging to the finest terminal branches and licking the clusters of flowers of *Crateva greveana* (Petter et al., 1975), a species with floral characteristics usually associated with bat-pollination (Sussman & Raven, 1978). *Phaner furcifer* also feeds on insect secretions, mainly exuded by homopteran larvae.

In addition to the presence of clawlike nails in *Phaner furcifer,* this species has a number of other morphological characteristics which seem to be related to gum feeding. These include special adaptations of the dentition, especially the upper incisors, canines, and premolars; specialized features of the digestive tract, especially the large size of the caecum; and a long, pointed tongue (Petter et al., 1971). Similar anatomical features are found in the African gum-feeder, *Galago elegantulus.*

FIGURE 7. *Lepilemur mustelinus.* (Photo by the author.)

Lepilemur mustelinus (Fig. 7) (referred to as *Lepilemur ruficaudatus* by Hladik et al., 1980), the fifth species of nocturnal primate at Marosalaza, is unusual for a small nocturnal primate (average adult = 600 g) in that it is a folivore. Its diet is made up almost exclusively of leaves. It has adaptations of the alimentary tract—a large caecum and wide colon (Le Gros Clark, 1959)—and of the dentition, especially the shearing crests of the molars (Kay et al., 1978), which are related to this dietary specialization.

Lepilemur diet has not been studied in detail at Marosalaza. Charles-Dominique & Hladik (1971) and Russell (1977), however, have done short-term but intensive studies of this species in a *Didierea* forest. The diet of *Lepilemur* is very restricted. Russell found that in a four-month period it fed on a total of 24 species of plant; an individual would feed on only 2–14 species per month. Two species accounted for 64% of the diet: *Alluadia procera* (52.8%) and *Grewia* sp. (11.1%). *Lepilemur* spent 91% of its feeding time ingesting leaves, 5.9% fruit, and 3.2% latex. No animal protein was eaten.

These nocturnal lemurs each have very specific

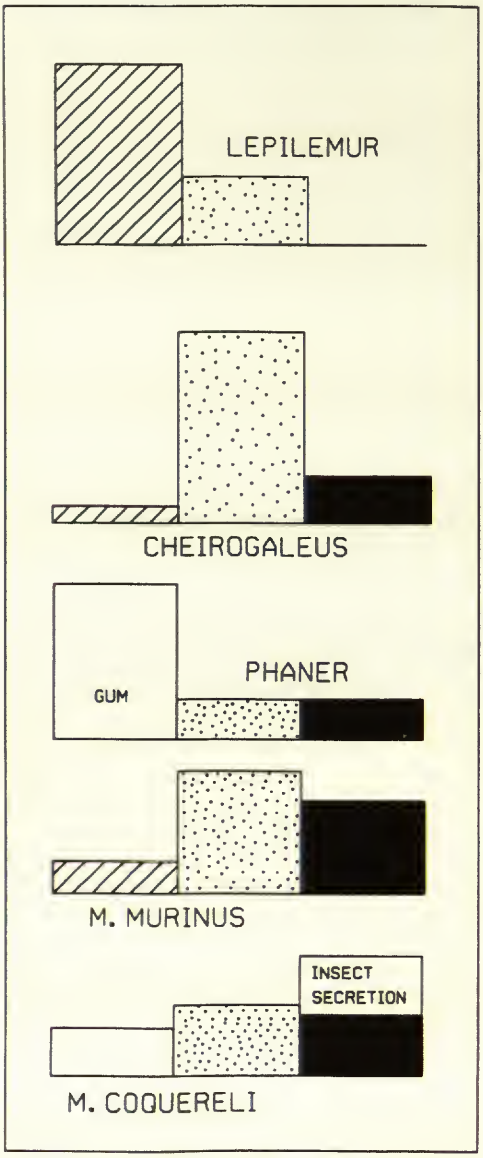

FIGURE 8. Summary of dietary differences between the nocturnal species at Marosalaza forest. Bars represent relative proportions of the diet consisting of leaves and/or gum (left), fruit (center), and animal matter (right). (Adapted from Hladik et al., 1980.)

diets (Fig. 8) and habitat choices, which would seem to minimize competition between species. The dietary pattern of each species can be related to specific morphological and physiological characteristics. In this seasonal forest, three of the species have diets that enable them to have a

FIGURE 9. The southwestern subspecies of the brown lemur (*Lemur fulvus rufus*). (Photo by the author.)

stable food source even during the severe dry season, when resources are generally limited: *Phaner* is a specialized gum feeder; *Lepilemur* a specialized leaf eater; and *Mirza coquereli* feeds mainly on insect secretions. During the dry season *Microcebus murinus* greatly reduces its activity and *Cheirogaleus medius* hibernates. During the wet season (austral summer November–April), when all five species are active, there is a maximum amount of food available. Furthermore, *M. coquereli* and *C. medius* are the only species which seem to feed in similar heights and biotopes. *Phaner* searches for insects and fruits higher in the canopy and *M. murinus* is found mainly in the lower bushes of secondary vegetation on the forest edge. *Lepilemur* is the only nocturnal species of Lemuriformes (except possibly *Avahi*) that eats an appreciable quantity of leaves. The feeding behavior of these relatively small, nocturnal primates of western and southern Madagascar seems to be well adapted to the long, seasonal shortages that occur in the deciduous forests during the dry austral winter.

All five of the nocturnal species present in the Marosalaza forest have a wide geographical distribution on Madagascar and are found in a variety of habitat types (Petter et al., 1977). Besides

FIGURE 10. The ring-tailed lemur (*Lemur catta*). (Photo by the author.)

the comparative study at Marosalaza, short-term studies have been conducted on *Murza coquereli* in a secondary *Anacardium* forest (Andrianarivo, 1981), on *Lepilemur mustelinus* in a desertlike *Didierea* forest (Charles-Dominique & Hladik, 1971; Russell, 1977), and *Microcebus murinus* mainly in a littoral forest zone (Martin, 1972, 1973). Even though these species show some species-specific patterns of behavior and habitat selection, generalizations concerning them should be made with caution since they have not been studied throughout their range and information presently available must be considered to be preliminary.

THE ECOLOGY OF DIURNAL LEMURS OF SOUTHWESTERN MADAGASCAR

Lemur catta, L. fulvus, and *Propithecus verreauxi* have all been the subject of long-term field studies. These three species have different habitat preferences, both from the nocturnal forms and from each other. Differences are most apparent in their use of vertical strata and in their diets, and in this paper I will concentrate on these two aspects of their behavior. Methods used to collect and analyze the data have been presented

TABLE 3. Total percentage of time in different forest strata by diurnal species inhabiting the southwest. 1 = ground level; 2 = small bushes; 3 = small trees and vertical trunks; 4 = continuous canopy; 5 = emergent layer.

Species	Stratum				
	1	2	3	4	5
Lemur fulvus	1	3	9	71	16
Lemur catta	33	13	23	25	6
Propithecus verreauxi	0	7	27	32	35

TABLE 4. Percentage of travel in different forest strata by diurnal species inhabiting the southwest.

Species	Stratum				
	1	2	3	4	5
Lemur fulvus	<1	2	4	85	8
Lemur catta	68	4	9	17	1
Propithecus verreauxi	0	9	50	22	19

TABLE 5. Percentage of feeding in different forest strata by diurnal species inhabiting the southwest.

Species	Stratum				
	1	2	3	4	5
Lemur fulvus	1	7	10	52	29
Lemur catta	29	14	33	16	8
Propithecus verreauxi	0	5	10	28	57

in detail elsewhere (Sussman, 1977; Richard, 1978).

Lemur fulvus and *L. catta* (Figs. 9, 10) are both quadrupedal, cat-sized animals (about 2,500 g) and in general morphology are very similar. However, they use the forest strata in very different ways. *Lemur fulvus* spends most of its day (greater than 70%) in the continuous canopy of the forest (level 4, Table 3) and almost never comes to the ground (level 1). This lemur is rarely seen in areas of the forest that would necessitate travel on the ground. *Lemur catta* utilizes all levels of the forest and spends a third of its time on the ground. It is often found in open areas of the forest or in dense vegetation. Where studied in sympatry with *L. fulvus*, the ring-tailed lemur, *L. catta*, spent 58% of the time outside the portion of the forest with a continuous canopy. *Propithecus verreauxi*, the sifaka, is much larger than the other two species (3–5 kg) and is a vertical-clinger-and-leaper (Fig. 11). Like the brown lemur, *L. fulvus*, it rarely comes to the ground. However, the sifaka spends much less time in the canopy level than *L. fulvus* and much more time on the vertical supports below the canopy (level 3) or in the emergent layer (level 5).

FIGURE 11. The southwestern subspecies of sifaka (*Propithecus verreauxi verreauxi*). (Photo by the author.)

These differences in use of vertical strata are accentuated when the level at which the three species do most of their group travel and where they feed is considered. Eighty-five percent of the travel of the brown lemur takes place in the

TABLE 6. Feeding patterns of diurnal species inhabiting southwestern Madagascar. Data from Sussman (1977) and Richard (1978).

	Total Number Species Eaten	% Most Eaten Species	Number of Spp. Over 80% of Diet	Wet Season			Dry Season		
				% Fruit & Flowers	% Leaves	% Other	% Fruit & Flowers	% Leaves	% Other
Lemur fulvus	13	50–75	3	47	50	bark <1	10	90	bark <1
Lemur catta	45	23–24	8	66	24	herbs 6	42	44	herbs 15
Propithecus verreauxi	85	12	26	60–70	<20	bark <20	<20	ca. 80	dead wood 5

canopy, whereas almost 70% of the ring-tail's is on the ground (Table 4). Due to its vertical clinging locomotion, the sifaka travels mainly on the vertical trunks below the canopy (level 3). The ring-tailed lemur feeds mainly on the ground and in the low trees, whereas the brown lemur and the sifaka feed in the canopy and emergent layers (Table 5). Over 50% of the *L. fulvus* diet comes from the canopy, and over 50% of that of *P. verreauxi* is found in the emergents.

Besides eating in different places, the three species have very different diets. *Propithecus verreauxi* and the southwestern subspecies of *Lemur fulvus* are folivorous and in the dry season 80–90% of their diet consists of leaves (Table 6). However, the two species have very different patterns of folivory. *Lemur fulvus* depends mainly on abundant plant species and has a very monotonous diet throughout the year. In both seasons, only 13 species of plant were eaten and three species made up over 80% of the diet. In the dry season the brown lemur's diet becomes even more specialized, with 75% of the diet made up of the leaves of *Tamarindus indica,* which dominates the riparian forests of the southwest (Sussman, 1977). *Propithecus verreauxi* has an extremely diverse diet and constantly checks on new plants and plant parts. In one group, 85 species were eaten over the year and 26 species made up 80% of the diet. Most plant species were eaten less than 1% of the time (Richard, 1978). Unlike *L. fulvus,* the diet of *P. verreauxi* becomes more diverse in the dry season and the leaves of more plant species are tested. *Lemur catta* is a frugivore and even in the dry season almost 60% of the diet consists of fruit and herbs. The ring-tailed lemur is intermediate between the other two species in dietary diversity (Table 6).

Thus, the sifaka is morphologically adapted to feed on leaves, yet its diet is much more diverse than the more specialized folivorous diet of *L. fulvus. Lemur catta* is generally frugivorous throughout the year. These three species also have different locomotor adaptations and abilities, and it is these adaptations which are probably most related to their distribution in different forest types in regions where their populations overlap. All three species coexist in the rich deciduous, canopy forests of the southwestern and southern portions of the occidental zone of Madagascar. However, *L. fulvus* is strictly arboreal and is found only in canopy forests. *Lemur catta* can also exploit forest edges, the thick brush and scrub forests common to this region, as well as the mountainous rocky regions of the central plateau. These areas necessitate terrestrial locomotion. The vertical clinging and leaping of *P. verreauxi* is a sufficient mode of locomotion for the canopy forests but it is also very likely a necessary adaptation for exploiting the desertlike *Didierea* forests of the south. *Propithecus* and the nocturnal *Lepilemur* are the only lemurs found in these types of forest.

Although ecological interactions between other diurnal Lemuriformes have not been studied systematically, from the little that is known a great deal of variation exists. *Propithecus verreauxi* populations inhabiting the north of the island have different patterns of ranging and intergroup spacing than those living in the south, even though their dietary patterns are quite similar. These differences seem to be related to the distribtuion of food resources. Subspecies of *Lemur fulvus* living on the Comoro Islands are different from those living in southwestern Madagascar in diet, ranging behavior, and social structure and organization (Tattersall, 1977). The ecological and behavioral variation that exists within the genus *Lemur* and even between subspecies of *L. fulvus* seems to be enormous and these populations are ideal for testing hypotheses regarding relationships between ecology, morphology, and individual and social behavior.

Conclusions

The ecological preferences and community roles of most species of Malagasy lemurs are as yet unknown. Because of human exploitation, forests of Madagascar are receding rapidly and much more needs to be done. Even now our knowledge of lemur adaptations and their complete role in the ecological communities of Madagascar can never be fully understood, since some of the 14 species that have become extinct within the last 2,000 years were surely members of these communities.

The lemurs of Madagascar offer a unique opportunity for the study of primate evolution. Madagascar has been isolated from other major land forms for millions of years. The lemurs have spread over the island and adapted to the available natural forest habitats. They have done this without interference from the anthropoids, which evolved later and never reached Madagascar. The nocturnal species are probably very much like our earliest primate relatives. Diurnal Lemuriformes have also been successful in Madagascar,

most likely due to lack of competition from anthropoids, and have filled many of the ecological roles that monkeys and apes occupy in Africa, Asia, and the Americas. These species allow us to study an adaptive radiation of primates completely different from, but parallel to and often convergent with, the anthropoids.

After surviving for 60 million years, many of the lemurs have become extinct, and as yet we know very little about the surviving forms. Essentially nothing is known about the communities of the north and east. What we do know, however, is intriguing and should encourage increased research and efforts to conserve what remains of the natural flora and fauna of this remarkable island.

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REPRODUCTIVE BIOLOGY AND CHALCID SYMBIOSIS IN *FICUS BURTT-DAVYI* (MORACEAE)[1]

HIMANSU BAIJNATH[2] AND SHAMILLA RAMCHARUN[3]

ABSTRACT

The pollination biology of *Ficus burtt-davyi* Hutch. is somewhat similar to that of *Ficus vogelii* (Miq.) Miq. (Newton & Lomo, 1979). The pollinator is an undescribed species of *Elisabethiella* Grandi. Four other species of chalcids (*Phagoblastus* sp., *Otitesella* sp., *Philotrypesis* sp., and *Sycoryctes* sp.) encountered in the syconia of *F. burtt-davyi* reduce the energy budget of the plant–pollinator mutualism. Initiation and maturation of the syconia of each crop were staggered over 3–4 weeks in this species. Female flowers averaged 94% per syconium of which 75% formed insect galls. The percentage of infestation by nonpollinators averaged 11% per syconium. A comparison of the style and ovipositor lengths of the respective partners displayed an anomalous pattern in this species relationship.

RÉSUMÉ

Le syndrome de pollinisation de *Ficus burtt-davyi* Hutch. ressemble en gros à celui de *Ficus vogelii* (Miq.) Miq. (Newton & Lomo, 1979). Le pollinisateur est une espèce non-décrite d'*Elisabethiella* Grandi. Quatre autres espèces de Chalcidae (*Phagoblastus* sp., *Otitesella* sp., *Philotrypesis* sp., et *Sycoryctes* sp.) trouvaient dans les syconiums de *F. burtt-davyi* réduisent le budget énergique du mutualisme entre la plante et son pollinisateur. L'initiation et la maturation de chaque groupe de syconiums etait étalé sur une période de 2–3 semaines dans cette espèce. Les syconiums contenaient une moyenne de 94% fleurs femelles dont 75% formaient des galles d'insecte. Le pourcentage moyen d'infection par des non-pollinisateurs etait de 11% par syconium. Une comparaison des longeurs de styles et d'ovipositeurs des partenaires respectifs a démonté des anomalies dans cette espèce.

Ficus L. (Moraceae) is a large woody genus that occurs throughout the tropics and subtropics of both hemispheres, with numerous species in tropical Africa. About 25 species occur in southern Africa. *Ficus burtt-davyi* Hutch., subgenus *Bibracteatae* Mildbr. and Burret, is distributed mainly along the east coast of southern Africa and extends into central Africa. Its growth form varies from a scandent bush to a small tree.

The obligatory mutualism involving species of *Ficus* and their agaonid (Hymenoptera, Chalcidoidea) pollinators is now well known to pollination biologists. In its broad details the pollination syndrome is somewhat similar in the different species studied. However, considerable variation in details of pollinator behavior, structural adaptations, sex ratios of pollinators and flowers, anther dehiscence, and seed production makes the pollination syndrome of each species of *Ficus* unique.

MATERIALS AND METHODS

Most of the studies were carried out in the extensive population of *Ficus burtt-davyi* located in the Bluff area, south of Durban in Natal. Details of the developmental cycle of the syconium were recorded by daily measurements of 25 marked syconia on a plant located on the campus of the University of Durban–Westville. Male and female flowers were fixed in FAA (formalin/acetic acid/alcohol) for morphological investigations. The materials for SEM study were dehydrated in an alcohol series, critical point dried, and gold coated.

Insects entering female phase syconia were preserved in 70% alcohol. Some of these were placed in a cotton blue–lactophenol mixture in order to pinpoint the position of pollen grains. Insect behavior was recorded by splitting open female and male phase syconia and observing

[1] We are grateful to the C.S.I.R. and the Research Fund of the University of Durban–Westville for financial support for the "Fig-Project." The wasps have been identified by Professor Wiebes and Mrs. Ulenberg and we are indebted to them for their interest and cooperation. The help of the staff of the Botany Department and the photographic assistance of Mrs. L. van Hooff is much appreciated. Mrs. R. Bunsee kindly undertook the typing.

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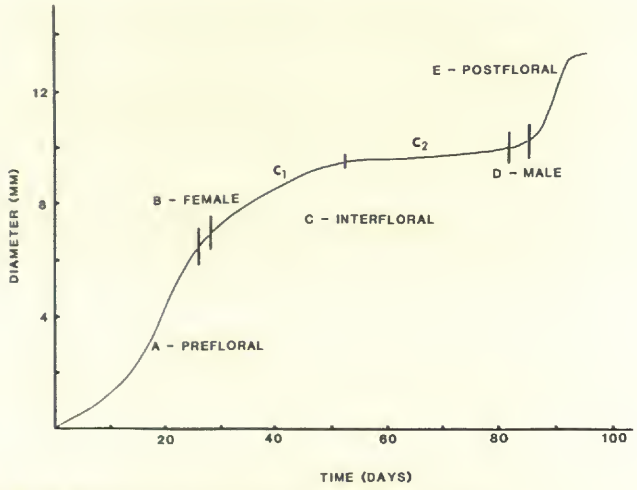


FIGURE 1. The developmental cycle of the syconium of *F. burtt-davyi.*

under the dissecting microscope. In addition, field observations were made to ascertain times of insect activity during the developmental cycle. Mass collections of insects were obtained by placing male phase syconia in Erlenmeyer flasks sealed with muslin cloth.

In a separate study, 20 syconia were harvested prior to insect emergence at the male phase and fixed in FAA. The numbers of male flowers and seed, gall, and degenerate female flowers were counted in each syconium.

In a further study, 15 syconia were collected at the male phase prior to completion of an exit channel to the exterior. Each syconium was isolated in an Erlenmeyer flask sealed with muslin cloth, and the insects were allowed to emerge. After four days a drop of chloroform was introduced into each flask to kill the insects. Insects remaining within the syconium were removed and the composition of the fauna of each syconium was recorded.

The style lengths of a sample of 200 female flowers from a syconium were measured. Measurements of the ovipositor lengths of 100 pollinating females were also undertaken. These measurements were divided into size classes, and the percentages were graphically represented.

RESULTS

MORPHOLOGY

In *Ficus burtt-davyi,* syconia are borne in pairs in the axils of leaves on young branchlets. Initially each pair of syconia is completely covered by a common bract that abscises when the syconia are about 0.5 mm in diameter. Each syconium is subtended by a small papery bract. Syconia are almost globose with an elongated slitlike ostiole. The two innermost ostiolar bracts descending from the pore into the syconium are much enlarged, green, and five or six cells thick. The passage into the syconium occurs between these two bracts. The remaining bracts are small, whitish, and one or two cells thick.

The male flowers are irregularly dispersed among the female flowers within the syconium. Each male flower is sessile and has three membranous perianth segments that enclose the single anther until anthesis occurs during the male phase of syconial development. The filament is short and fleshy; the bithecate anther lobes dehisce longitudinally. The female flowers are typical of the genus, each consisting of three membranous perianth segments and a uniovulate ovary with a laterally attached style. There is the usual staggering of style and pedicel lengths, and a loose synstigma is present. Each stigma is bilobed and highly papillate.

FLOWERING

The five phases of development of the syconium (Galil & Eisikowitch, 1968) can be recognized in *Ficus burtt-davyi* (Fig. 1), and these will be detailed very briefly.

The prefloral phase is fairly long, with the fe-

TABLE 1. Summary of characters and behavior of the chalcid wasp fauna infecting the syconia.

Taxon	Group	Oviposition	Sexual Dimorphism	Copulation
Elisabethiella sp.	Pollinator	At female stage down style	Very pronounced	In gall of female wasp
Otitesella sp.	Parasite	At prefloral stage via wall	Very pronounced	In syconial cavity
Phagoblastus sp.	Parasite	?	Less obvious, winged males	Outside on syconial wall
Philotrypesis sp.	Inquiline	At interfloral stage via wall	Very pronounced, males rarely winged	In syconial cavity
Sycoryctes sp.	Inquiline	At interfloral stage via wall	Very pronounced	In syconial cavity

male phase being attained after about 25 days, at which stage the female flowers are mature and the stigmas receptive. The syconia remain in the female phase for about two days, after which the ostioles become sealed by a sticky exudate and the syconia enter the interfloral stage, which lasts approximately 53–55 days. The two subphases of the interfloral stage (Fig. 1), during which the growth rates alter (Baijnath & Ramcharun, 1983), were also noted in this species. During the male phase, which lasts about four days, eclosion of the chalcids occurs and the anther lobes of the staminate flower dehisce longitudinally. During the postfloral period of 7–8 days there is a rapid increase in diameter, accompanied by the ripening of the syconial wall.

It was noted from the study sample that flowering was asynchronous or nonseasonal. However, in the warmer months many more plants bore syconia at any one time and crops were generally larger than in cooler months. In *Ficus burtt-davyi* syconial initiation was staggered over a period of 3–4 weeks. This resulted in syconia of different ages being present on a tree at a particular time, often on a single branchlet (Fig. 2). The presence of crop overlap, i.e., initiation of new crops of syconia prior to completion of the development of the syconia of the previous crop, also results in syconia of many developmental phases being present on a tree at a particular time.

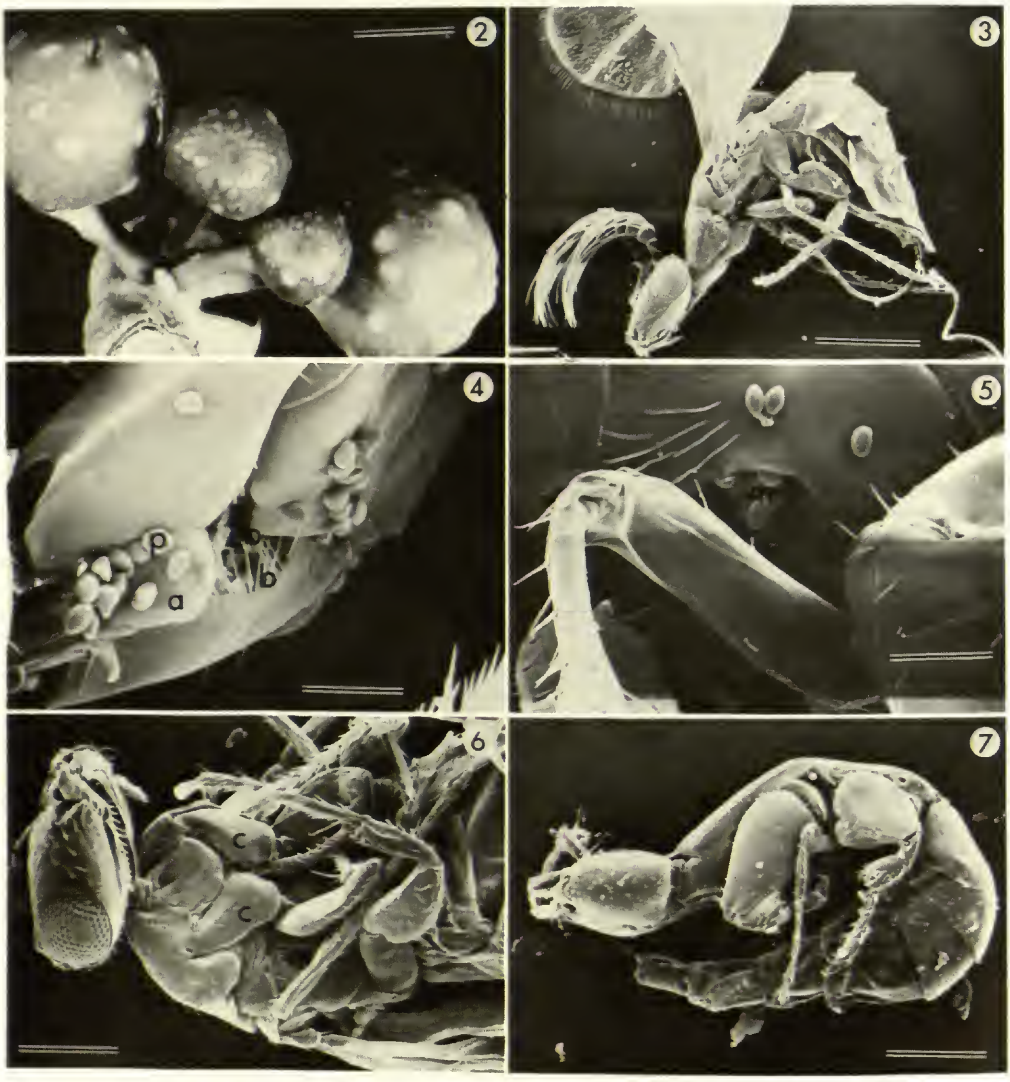
Abortive syconia collected from beneath the plants indicated that these had not been infected by insects. However, this was not confirmed by experimentally isolating syconia in order to prevent infection.

FIG INSECTS

At least five taxa of chalcid wasps have been isolated from syconia of *Ficus burtt-davyi,* all of which are considered to be new species (Wiebes, pers. comm.). Some of the characteristics of each taxon are summarized in Table 1.

Elisabethiella sp. (family Agaonidae). As is typical of agaonids, this species displays striking sexual dimorphism. The female is a small black alate insect about 1 mm long with well-developed eyes and antennae (Fig. 3).

Female pollinators force their way into the syconium through the ostiole at the female phase of syconial development. They possess specialized pollen-carrying structures, the coxal corbicula (Fig. 4) and the mesothoracic pockets (Fig. 5). On entry into the syconium, females move about on the synstigma with their antennae touching the stigmatic surface. The partly extended ovipositor is supported within the triangular flap (hypopygium) which is held away from the body at right angles to the ventral surface. This results in a complete curving of the abdomen. The ovipositor is then extended into a style and while ovipositing, the prothoracic legs are moved backwards towards the coxal corbicula. At this stage the coxae are held away from the ventral surface, thus allowing easy access to the pollen grains. Pollen is scooped out of the corbicula by the arolia, which also pick up pollen from the mesothoracic pockets as they continue this backward movement. The arolia are then stroked onto the stigmas in front of the insect, thus effecting pollination. This act involves alternate movements of the prothoracic legs and is repeated 6–10 times.



FIGURES 2–7. 2. Branchlet of *F. burtt-davyi* illustrating syconia at different stages of maturity. Scale = 3 mm. 3–7. The pollinator *Elisabethiella* in *F. burtt-davyi*.—3. Side view of female pollinator. Scale = 0.2 mm.—4. Part view of prothoracic leg of the female pollinator. a, arolium; b, bristles; cb, corbiculum; p, pollen. Scale = 0.08 mm.—5. Part view of the ventral surface of the female pollinator. m, mesothoracic pocket. Scale = 0.8 mm.—6. Ventral view of anterior part of the female pollinator. c, coxa; m, mesothoracic pocket. Scale = 0.4 mm.—7. Side view of the male pollinator. Scale = 0.06 mm.

Pollen loading also involves alternate movements of the legs, with each leg making an average of 22 scoops. After emerging from their galls the females approach the already dehisced anthers and widen the slits with their mandibles if necessary. The pollen grains are scooped by the arolia, which move backward to the mesothoracic pockets. Some pollen is brushed into these pockets, but the bulk is carried forward to the very large hollow coxal corbicula. The median margin of each corbiculum is lined by a row of stiff bristles that aid in removal of pollen from the arolium during pollen loading and assist in holding the pollen grains within the corbiculum (Fig. 4). Three to four similar bristles occur on the anterior margin of the mesothoracic pockets (Fig. 6).

The males of *Elisabethiella* are minute, brown,

wingless, and blind. They have reduced antennae but well-developed mandibles. The abdomen of the male is telescoped into an extensible solenogaster, which is curved underneath the thorax and directed anteriorly (Fig. 7). This allows fertilization of the females through the small opening that is bitten in the walls of the galls containing the females. The aggressive behavior sometimes displayed by agaonid males was not observed in *Elisabethiella*. The males bite a channel to the exterior in the region of the ostiole to allow escape of the fig insects. The males become very inactive as soon as the exit channel is complete and die within a few hours.

Phagoblastus sp. (family Torymidae). The females of *Phagoblastus* are somewhat similar to the males except that the former are black, while the latter are light brown. Both sexes are winged, have well-developed eyes and antennae, and have conspicuous mandibles with a characteristic subapical tooth. Ovipositing by females of *Phagoblastus* was not observed. Although numerous female phase syconia were examined, females of *Phagoblastus* were not found within the syconial cavity.

The males emerge from their galls during the latter part of the male phase and fly out through the existing exit channel. They gather on the outer wall of the syconium and await the females which appear a little later. As the females emerge through the exit channel, they are caught from behind and copulation occurs as the males bend their abdomens forward while grasping the abdomens of the females with their prothoracic legs. In this species the males do not assist the females in the emergence from their native galls. The females have equally well-developed mandibles and are capable of accomplishing this task. Although the males may be structurally capable of biting an exit channel to the exterior of the syconium, this does not appear to be a part of their behavioral sequence on eclosion. Two syconia that were found to contain an exclusive population of *Phagoblastus* remained sealed, and the insects perished within the cavity.

Otitesella sp. (family Pteromalidae). The females range from 1 to 2 mm in length and are dark, metallic green, and shiny. The eyes and antennae are well developed, and the mandibles are fairly large. The major part of the ovipositing apparatus is internal and therefore not visible as a long "tail." These insects oviposit through the syconial wall during the prefloral phase of syconial development when the syconia are about 4 mm in diameter (±19 days old).

Sexual dimorphism is pronounced in this genus. The males are brown and wingless but have fairly well-developed eyes and antennae. Two elongate setae bearing several branches are located on the mesothorax on either side of the body. The males display territorial behavior within the syconium. The slightest contact of the lateral setae between conspecific males resulted in aggressive fights involving vicious attacks with their very large and powerful mandibles.

On emerging from their galls, males move about in the syconial cavity and probe the galls with their antennae in search of females. The females slowly bite their way out of their native galls while the males watch closely. As soon as they emerge copulation occurs, with the males holding onto the thorax of the females in a manner that allows the ventral surfaces to come together.

Philotrypesis sp. (family Pteromalidae). The body of the female of *Philotrypesis* is about 1 mm long; but the extended ovipositor, which is sheathed by the lengthened eighth and ninth terga and the third valvula, is about 2.5 times the length of the body. The ovipositor valves pierce the syconial wall, thus inserting the ovipositor into position for egg laying. This occurs during the early interfloral period.

Sexual dimorphism is also pronounced in this species. The males are brown and wingless with reduced sensory structures but have elongate, well-developed limbs and are thus capable of very rapid movement. Fertilization occurs in a manner similar to that described in *Phagoblastus*, but inside the syconium.

Sycoryctes sp. (family Pteromalidae). The females are small, blue-black, and similar in size to *Philotrypesis*. The ovipositor is sheathed by the lengthened ninth tergum and the third valvula, and is about three times the length of the body. Oviposition occurs during the early interfloral phase. The males in this species are somewhat similar to the males of *Philotrypesis*.

FLORAL RATIOS AND SEED PRODUCTION

The counts of male and female (seed, gall, and degenerate) flowers in 20 syconia (Table 2) indicated an average of 94% female flowers per syconium; the remaining 6% were male. A very small percentage of female flowers degenerate, while most form galls. The percentage of female

TABLE 2. Floral composition of the syconium at late C phase based on a count of 20 syconia.

Sycone Number	Female Flowers				Male Flowers
	Gall	Seed	Degenerate	Total	
1	156	40	3	199	10
2	143	35	6	184	13
3	161	37	5	203	15
4	154	43	7	204	12
5	166	43	6	215	14
6	147	53	2	202	11
7	134	31	14	179	10
8	158	41	4	203	11
9	151	41	6	198	13
10	163	47	2	212	16
11	139	48	7	194	14
12	139	44	3	186	12
13	159	63	4	226	16
14	147	51	3	201	14
15	143	50	4	197	12
16	145	50	3	198	12
17	159	54	6	219	14
18	164	56	6	226	16
19	171	53	4	228	15
20	146	43	7	196	12
Average*	152 (75)	46 (23)	5 (3)	204 (94)	13 (6)

* Percentage in parentheses.

flowers that eventually set seed averages 23% per syconium.

INSECT RATIOS

The ratios of males and females of the pollinating wasps parallel the situation recorded for the fig flowers (Table 3). Most of the galls within the syconia contained individuals of the pollinating wasp. In these counts the percentage infestation by parasites and inquilines averaged 11%. However, it must be noted that a fair amount of variation in this ratio does occur and occasionally the numbers of parasites and inquilines exceed those of the individuals of *Elisabethiella* within a syconium. Such situations, however, do not appear to be very common from our observations.

FLORAL DIMORPHISM AND POLLINATOR INFESTATION

In *Ficus burtt-davyi* it was observed that the occurrence of individuals of the pollinating species in sessile or long-styled flowers was fairly common. It has been found in previous studies (Newton & Lomo, 1979; Baijnath & Ramcharun, 1983) that the presence of long-styled flowers was of great significance, since the pollinating wasps were not capable of infesting them and this ensured that a percentage of the female flowers set seed. Measurements of style and ovipositor lengths of the respective partners in this symbiosis displayed an anomalous pattern (Fig. 8). It was found that a fair percentage of the sample of the pollinating species possessed ovipositors that were long enough to allow infestation of the longest styled flowers. In *F. burtt-davyi* an additional floral dimorphism was noted. Long-styled flowers were found to possess much smaller ovaries than short-styled flowers.

DISCUSSION AND CONCLUSIONS

Sexual reproduction in *Ficus burtt-davyi* is completely dependent on the mutualistic relationship with the agaonid wasp *Elisabethiella* sp. The relationship is based on a finely co-evolved system involving extensive morphological, physiological, and chemical co-adaptation between the partners.

The reproductive biology of the partners includes a series of perfectly synchronized stages that ensure the production of new generations of individuals of both mutualistic partners. *Ficus*

TABLE 3. A calculation of the percentage of females and males of the pollinator, together with the percentage of pollinators and parasites and inquilines in each syconium based on a count of 15 syconia.

Syconium Number	Female	Male	Pollinators	Parasites and Inquilines
1	92	8	91	9
2	86	14	89	11
3	89	11	75	25
4	90	10	93	7
5	82	18	100	0
6	89	11	85	15
7	83	17	96	4
8	72	28	90	10
9	96	4	86	14
10	87	13	84	16
11	88	12	92	8
12	92	8	90	10
13	86	14	87	13
14	81	19	97	3
15	93	7	83	17
Mean	87	13	89	11

vogelii (Miq.) Miq., which is also a member of the *Bibracteatae,* has been described in detail by Newton & Lomo (1979). It was found that the developmental cycle of *F. burtt-davyi* was approximately 33 days longer than that of *F. vogelii.* However, it was noted that in warm weather the rate of development during the interfloral period increased slightly, resulting in completion of the cycle 5–7 days earlier. The two subphases of the interfloral phase reported in *F. capensis* Thunb. (Baijnath & Ramcharun, 1983) were also found to be correlated with larval and pupal stages of development of the pollinating insect in *F. burtt-davyi.* The variation in the interfloral period according to prevailing weather conditions probably results from the alteration of the rate of insect development. The rapid increase in syconial diameter during the postfloral phase (Baijnath & Ramcharun, 1983) also occurred in *F. burtt-davyi* but was not reported in *F. vogelii.*

The asynchronous flowering pattern occurring in figs has been noted by numerous fig biologists, and a detailed study was carried out by Wharton et al. (1980). This phenomenon is essential for the maintenance of the pollinating species, since these are known to be nonfeeding and short lived. Females of *Elisabethiella* survived only 2–4 days in the laboratory.

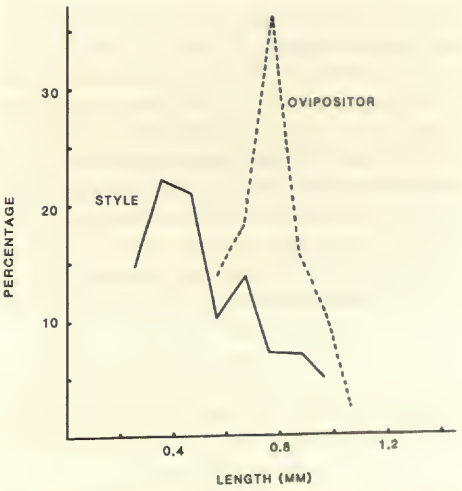


FIGURE 8. Size distributions of styles of *F. burtt-davyi* and ovipositors of the female of the pollinator *Elisabethiella* of *F. burtt-davyi.*

A few syconia infected by structurally aberrant females produced "seed" syconia in which seeds were present in both long- and short-styled flowers. Females with structural malformations were often observed to emerge from syconia a day or two later, and such individuals were also found to be in greater number in the last few syconia of a given crop. The presence of such seed syconia, together with the presence of pollinator galls in long-styled flowers, indicates that there is no bimodal distinction between the different types of female flowers. The significance of the larger ovaries in the short-styled flowers is not known. However, it is tempting to suggest that this may be an evolutionary step toward bimodal distinction between flowers, since in this species it was found that very often the pollinating females were capable of infecting long-styled flowers. In all other species of figs studied, it was found that a proportion of the flowers bore styles that were too long for wasp infestation, and this ensured seed production.

Otitesella oviposits into the syconium during the prefloral phase and appears to be capable of causing parthenocarpic fruit development. One ripe syconium carrying an exclusive population of dead males and females of *Otitesella* indicated that the behavioral sequence of the males of this species does not include the biting of an exit channel, although they are structurally capable of performing this task. In the absence of males

of *Elisabethiella* these insects remain entrapped within the syconium.

The reduction in flowering during the winter months would result in a decline of pollinator populations and seed production. It was found, however, that although trees may often be recorded as being in a nonreproductive state, careful observation almost always revealed the presence of a few (often less than 10) syconia. It is believed that such flowering is of great significance in further ensuring pollinator survival.

In the different species of figs studied (Galil & Eisikowitch, 1968; Newton & Lomo, 1979; Wharton et al., 1980; Baijnath & Ramcharun, 1983) it has been found that syconia were usually produced in distinct crops in which all the syconia matured almost simultaneously. In *Ficus burtt-davyi* initiation and final maturation of the syconia were staggered over 3–4 weeks. This phenomenon provides a greater advantage to the fig–wasp symbiosis, since pollen-carrying females are released over a 3–4 week period for each crop. This greatly increases the chances of female pollinators finding receptive figs, as this phase lasts for only 1–2 days.

The existence of crop overlap as reported for *Ficus capensis* (Baijnath & Ramcharun, 1983) also occurred in *Ficus burtt-davyi.* Outcrossing is therefore not obligatory, and inbreeding by geitonogamy must occur fairly frequently during the summer months when male and female phase syconia may be present on an individual tree. In this very specialized symbiosis genetic cohesion by such inbreeding is advantageous in maintaining the stability of the syndrome. Endogamous reproduction is also prevalent in *Elisabethiella* since mating commonly occurs between the offspring of a single female.

From its structural features *Phagoblastus* appears to be a parasite of the fig. Ovipositing by this insect was not observed and no further comment can be made. *Phagoblastus* sp. inhabiting *Ficus vogelii* (Newton & Lomo, 1979) was reported to enter the syconium at the female stage and to oviposit down the styles. In addition, pollination by this genus in *F. vogelii* appears to be the only report of a nonagaonid successfully pollinating a fig.

In all the species of chalcids found in *Ficus burtt-davyi,* with the exception of *Phagoblastus,* the males are somewhat reduced in structure, which can be related to their function. Copulation occurs within the syconial cavity, and males are wingless with reduced sensory structures. Their morphology enables efficient movement in the confined space within the cavity. The well-developed mandibles of males enable rapid eclosion from their native galls and in some species are used in aggressive territorial behavior. In males of *Elisabethiella* the mandibles also serve as tools for preparing an exit channel from the syconium.

In *Ficus burtt-davyi* the innermost ostiolar bracts form a chute into the syconium. Females of *Elisabethiella* entering the syconia do not have their antennae damaged. These structures come into contact with the synstigma during ovipositing and pollen unloading. The pollen-carrying structures ensure that sufficient pollen is carried into the syconium. In *Elisabethiella* the coxal corbicula appear to be the main pollen-carrying structures. The stiff bristles on the median edge of each coxa interlace to form an effective pollen container that is held against the ventral surface of the body.

The pollen grains of figs are small, thus allowing copious amounts to be carried by each pollinating female. The elongate stigmatic papillae appear to aid in pollen removal as the arolia are stroked onto them during the pollination act. The stigmatic structures of different figs appear to be related to pollinator behavior. In *Ficus capensis* the pollinator simply shovels pollen out of the pollen-carrying structures and the stigmatic papillae are very reduced.

Anther cutting behavior in males of *Elisabethiella* did not occur. This is probably unnecessary since the male flowers in the *Bibracteatae* are not localized and overcrowding of a particular area could not occur. In *Ficus vogelii* the pollinating females were reported to open anther sacs with their mandibles. In *F. burtt-davyi* anthers dehisced spontaneously, but the openings were widened by the females when necessary.

Philotrypesis and *Sycoryctes* oviposit from the outside through the wall of the syconium, and the elongate ovipositing apparatus is well designed for this. These insects do not affect seed productivity, as they are inquilines and parasitize galls. It is likely that they parasitize the galls of *Elisabethiella* sp., but this has not been confirmed experimentally. If this is the situation, then they would adversely affect the fig–pollinator mutualism since they reduce the numbers of pollinators produced.

In *Elisabethiella* (and other chalcids) many more females are produced as compared to the numbers of males. The males are polygamous.

This is cost effective since only the females are actually involved in pollination. A few males are sufficient to perform the task of impregnation and prepare an exit channel.

The number of female flowers produced per syconium far exceeds that of male flowers. The advantage of this is obvious, since only the female flowers account directly for seed and pollinator production. The few male flowers in each syconium produce copious amounts of small pollen grains that are deliberately collected by the pollinating insects and deposited onto the receptive stigmas. Since pollination is a deliberate act rather than a matter of chance, pollen production can be kept to a minimum, thus aiding in energy efficiency.

Approximately 75% of female flowers become infected by wasp larvae. Most of the galls are devoted to pollinator production. However, the presence of parasites and inquilines results in unfavorable energy loss. In general, parasitization in *Ficus burtt-davyi* in the study area was not marked. However, ratios of the unwanted symbionts do increase when fewer syconia are present in the population. The population therefore does bear increased energy losses at certain times.

Although figs produce large amounts of seeds, predation is very heavy (Slater, 1972; Baijnath et al., 1980). This would account for the relatively small population size in comparison to seed productivity. The mortalities of the chalcids occupying figs must also be high, since the insects are short lived and must find syconia of a very specific developmental stage within a short period of time. *Elisabethiella,* being short lived and small sized, displays a population biology typical of *r*-selected species in producing very large numbers of offspring.

Most of the species of *Ficus* are characterized by elaborate patterns of ethodynamic pollination. It is interesting to note that studies relating to the details of each partnership, the chalcid genera occupying the syconia, the behavior of chalcids, and the morphological co-adaptations can throw much light on evolutionary relationships among the chalcids and among the different species of *Ficus.*

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THE INTERACTION OF GYNOMONOECY, DICHOGAMY, AND WIND-POLLINATION IN *GUNNERA PERPENSA* L. (GUNNERACEAE) IN SOUTH AFRICA[1]

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ABSTRACT

Gunnera perpensa L. is the only member of the genus in Africa. Two populations growing near Johannesburg, South Africa, were studied to determine the sex expression, pollination system, and breeding system. The plants reproduce both asexually (by rhizomes) and sexually. The single inflorescence on a plant is gynomonoecious, contradicting previous reports of polygamomonoecy in the species. The elongated inflorescence consists of female flowers on the lower portion and bisexual flowers on the upper portion. The female flowers are strongly protogynous in relation to the bisexual flowers. The bisexual flowers are themselves strongly protandrous. Outcrossing is promoted in both floral types but some geitonogamy may occur in the female flowers. *Gunnera perpensa* is similar to other species of *Gunnera* in being wind pollinated as evidenced by the high pollen/ovule ratios, floral morphology, and starch storage in the pollen grains. Flower morph ratios are strongly female-biased ranging from 2.2 to 5.3 female/bisexual. The functional gender, however, ranges from 43% female to 60% female. The reproductive effort is overwhelmingly male-biased at the lower female gender values but nearly equal at the highest female gender values. In a wind-pollinated plant, gynomonoecy is an economical system of regulating functional gender when the male reproductive effort is large. Adding large numbers of female flowers does not drastically change the functional gender ratio but the cost is considerably less than adding hermaphrodite flowers. Dichogamy may function to prevent stigma clogging while promoting outcrossing.

RÉSUMÉ

Gunnera perpensa L. est le seul membre du genre en Afrique. Les auteurs ont étudié deux populations qui poussent près de Johannesburg en Afrique du Sud afin de déterminer l'expression sexuelle, le syndrome de pollinisation, et le système de fecondation. Les plantes se reproduisent à la fois asexuellement (par des rhizomes) et sexuellement. La seule inflorescence de cette plante est gynomonoïque, ce qui va à l'encontre des compte-rendus précédents qui la signalait comme polygamomonoïque. L'inflorescence allongée consiste en des fleurs femelles sur la portion inférieure et des fleurs bisexuelles sur la portion supérieure. Les fleurs femelles sont fortement protogyniques par rapport aux fleurs bisexuelles. Les fleurs bisexuelles elle-mêmes sont très protandres. La pollinisation croisée est favorisée dans les deux types floraux mais la geitonogamie peut aussi se produire dans les fleurs femelles. *Gunnera perpensa*, qui est pollinisée par le vent, ressemble en cela à d'autres taxons du genre, comme en témoignent les rapports pollen/ovule élevés, la morphologie florale, et l'accumulation d'amidon dans les pollens. Les morphes femelles sont prédominants; les rapports femelle/bisexuel varient de 2,2 à 5,3. Cependant, le sexe fonctionel peut varier de 43% femelle à 60% femelle. La gynomonoécie chez les plantes anémophiles représente un syndrome économique pour régler le sexe fontionnel quand l'effort reproductif mâle est élevé. L'addition d'un nombre important de fleurs femelles ne modifie pas fortement le rapport de sexe fonctionnel, mais le coût est bien moindre comparé à l'addition de fleurs hermaphrodites. Il est possible que la dichogamie fonctionne de manière à éviter l'encombrement des stigmates en même temps qu'elle favorise la pollinisation croisée.

Gunnera perpensa L. (Gunneraceae) is a rhizomatous perennial herb occurring from Ethiopia and the Sudan southwards through East Africa to the Cape in South Africa. It also occurs in Madagascar. It is the sole African species of *Gunnera*, which otherwise has major concentrations of species in New Zealand, South and Central America, and the Hawaiian Islands (Bader, 1961). Most taxonomic treatments of the African species indicate that it is polygamomonoecious (each plant having a mixture of male, female, and hermaphrodite flowers) (Boutique & Verd-

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court, 1973; Schindler, 1905). Casual observations of populations in the field in South Africa, however, suggest that rather than being polygamomonoecious they are strictly gynomonoecious as noted by Adamson (1950).

Gynomonoecism is not unknown in the genus (Palkovic, 1978; Webb, pers. comm.), but it is a rare form of sex expression in the flowering plants generally known only from five or six families (Yampolsky & Yampolsky, 1922; McComb, 1966). Interestingly, it is fairly common in the Compositae (Lloyd, 1979). Despite the current interest in the evolution and adaptive value of sex expression of plants, little is known regarding gynomonoecy.

Although there is a lack of hard data to explain the adaptive significance of gynomonoecy, several hypotheses have been advanced (mostly to account for its relatively high frequency of occurrence in the Compositae). Willson (1983) suggests that because the female flowers are on the periphery of heads in the Compositae they will receive outcross pollen when pollinators arrive from other plants. Thus gynomonoecy can function to facilitate outcrossing. Bawa & Beach (1981) suggest that gynomonoecy functions primarily as a pollination system rather than as an outcrossing system, at least in the Compositae. Finally, Lloyd (1979) argues that gynomonoecy is an economical method of increasing parental success by adding female flowers. He suggests that if there are effective pollen presentation and transferral mechanisms, increasing male effort along with female effort in the form of bisexual flowers would be uneconomical.

Since there are few detailed studies of gynomonoecy even in the Compositae (with the exception of Lloyd, 1972a, 1972b) we decided to investigate gynomonoecy in *Gunnera perpensa*. The observations and experiments reported here attempt to test several of the hypotheses advanced to explain the function of gynonomoecy in plant groups, particularly in the Compositae. Firstly, does gynomonoecy facilitate outcrossing in *G. perpensa*, perhaps by having temporal separation of floral morph maturation? Secondly, what is the pollination system; is it wind pollinated as are other *Gunnera*s (Palkovic, 1978)? How does the sex expression function in relation to the pollination system, especially if the species is wind pollinated? What are the floral morph ratios? Are they equal or biased, and does this appear to maximize parental success? Finally, do the floral morph ratios correlate well with estimates of functional gender and reproductive effort for the different sexual functions?

Methods of Study

Two populations of *Gunnera perpensa* were studied during spring and summer of 1984. The populations grow along a small stream in the northwestern edge of Johannesburg, South Africa. They are separated by about 20 m and contain approximately 160 and 300 individuals, respectively. Ten inflorescences (five in each population) were marked and studied to determine the floral maturation sequence. Twenty-four inflorescences, 12 from each population, were marked for use in determining the proportion of hermaphrodite (☿) and female (♀) flowers and for studying the pollination biology. All were in a similar stage of maturity at the beginning of the experiments.

The 24 inflorescences were divided into four treatments. Treatment UT consisted of eight inflorescences that were marked and otherwise untreated. At fruit maturity these inflorescences were removed from the plants and each was divided into female and hermaphrodite portions. There is a sharp demarcation between the female and hermaphrodite flowers on the inflorescence (Fig. 1), so that they are easily separated. The 16 separate lots were air dried and the fruits were then harvested and weighed. Five samples of 50 fruits from each lot were weighed. The weights were averaged for each lot and used to obtain both an estimate of the total number of flowers (and fruits) produced by each section of the inflorescence and an estimate of the floral morph ratios on the entire inflorescence.

In addition to the calculation of the morphological gender (female/hermaphrodite flower ratios), the functional gender is also calculated (Lloyd, 1979, 1980). The concept of functional gender according to Lloyd (1979) is defined as the proportions of the parental fitness transmitted through its ovules and pollen. It attempts to measure the parental performance of a plant as well as provide a quantitative measure of sex. Both the functional femaleness of a plant, termed G_i, and the functional maleness of a plant, termed A_i, can be estimated by the equations:

$$G_i = \frac{gi}{gi + aiE} \quad \text{and} \quad A_i = \frac{aiE}{gi + aiE},$$

where gi is the gynoecial production, ai is the androecial production, and E is an equivalence

function to relate pollen and seed production to each other. The equivalence function is estimated by:

$$E = \frac{i^{gi}}{i^{ai}}.$$

In this study we use the number of female flowers + hermaphrodite flowers to give a value for gi and the number of hermaphrodite flowers only for ai.

In order to examine the reproductive effort expended on the female and male functions we have used the method developed by Lemen (1980) for wind-pollinated plants. He estimated the relative male effort by the function:

$$RME = C\frac{\text{Total anther volume on a plant}}{\text{Total seed weight on plant}},$$

where C is a correction factor to relate energetic cost in seed weight to cost in anther volume. Lemen (1980) estimated a value for C of 0.6783, which we use here. This value was estimated from data derived from *Amaranthus* species (see Lemen, 1980, for discussion of its applicability).

Treatment EU was used to test for possible differences in fruit set and fruit weight due to removal of the hermaphrodite flowers and for the effectiveness of outcrossing in the female flowers. The treatment consisted of eight inflorescences that were effectively emasculated by cutting off the top portion of the inflorescence containing the hermaphrodite flowers. These inflorescences were otherwise untreated and left to mature.

Treatment EB was used to test for fruit set in covered inflorescences that had been emasculated as in the EU treatment and thus were without hermaphrodite flowers. The inflorescences were also monitored to observe the maturation sequence of the stigmata in the absence of pollen. This treatment consisted of four inflorescences that were covered with cardboard cylinders after removal of hermaphrodite portions. The cylinders had their tops closed with nylon stocking that allowed air movement but excluded pollen.

Lastly, treatment UB consisted of four inflorescences that were covered but otherwise untreated to test for fruit set as a result of geitonogamy.

For all treatments the inflorescences were removed and the fruits harvested and weighed as before. Fruit set was assessed by fruit weights. The fruit weights from treatment A were used as the control and assumed to represent normal, mature fruits with embryos. Also, the sample sizes for the last two treatments were small, but we declined to involve any more inflorescences for fear of upsetting normal pollen flow.

FIGURE 1. Illustration of an inflorescence of *Gunnera perpensa* with the lower portion female and the upper hemaphrodite. Scale = 130 mm.

Pollen/ovule ratios were determined for four flowers on each of five inflorescences. The anthers from each flower were macerated in a known quantity of cotton blue–lactophenol. The number of pollen grains in the fluid was then estimated using a hemocytometer.

Pollen grains were tested for the presence of starch and lipids as nutritive reserves. Pollen was removed from freshly dehiscing anthers and stained with a potassium iodide solution (for detection of starch) and with Sudan IV (for detection of lipids) (Baker & Baker, 1983).

Pollen stainability as a measure of viability was determined in 10 inflorescences for each population. Five anthers from each inflorescence were removed just before dehiscence. The pollen was removed, bulked on a slide, and stained in cotton blue–lactophenol for a minimum of 12 hours. Five hundred grains from each inflorescence were counted and scored for fertility (fully stained) or sterility (unstained or weakly stained).

Results

Inflorescence morphology and floral development. *Gunnera perpensa* has a growth habit typical of the genus. It has creeping rhizomes and very short upright stems approaching acaulescence; the leaves are essentially basal. Preliminary observations suggest that each population might well represent a single clone since they are rhizomatous. Each "plant," which may be either a ramet or genet, normally only produces one large inflorescence that may attain a length of nearly one meter. The inflorescences appear after leaf expansion in spring. The inflorescence is a compound spike (Fig. 1). The sessile flowers are borne on simple branches (spikelets) spirally arranged on the main axis. There may be several hundred spikelets on the inflorescence, which is gynomonoecious, with the female flowers on the lower spikelets and the hermaphrodites on the upper (Fig. 1). Generally the spikelets have only one flower type but in very large inflorescences some of the female spikelets are tipped with hermaphrodite flowers. Additionally, there is a transition zone between the female and hermaphrodite spikelets where up to 10 spikelets may have a mixed arrangement of flower types. We observed no instances of female flowers occurring above the transition zone.

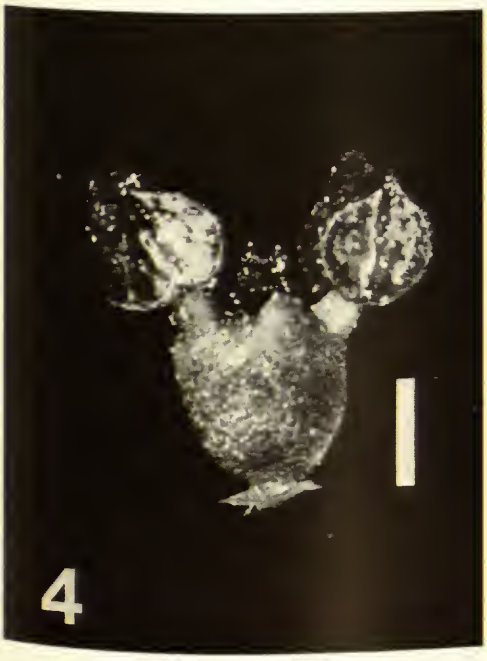
Both types of flowers are small (1–2 mm long) and are epigynous with short, nearly vestigial sepals (Figs. 2, 3). The female flowers are apetalous but the hermaphrodite flowers may or may not have small strap-shaped petals that are deciduous at anthesis. The hermaphrodite flowers have two stamens with anthers measuring 1 mm wide × 2 mm long. The stigmas are bifid and strongly plumose.

Floral maturation is acropetal, proceeding from the lowermost spikelets upward and from the bases of the spikelets to their apices. The female flowers are fully receptive 7–9 days before anthesis of the first hermaphrodite flowers. Counts of female spikelets from 25 different inflorescences at the time of anthesis of the first hermaphrodite flowers showed a mean of 76% ± 10% having flowers with withered stigmas (indicating pollination). Thus, although there is overlap between female stigma receptivity and hermaphrodite anther dehiscence, a large percentage of the females have already been pollinated with pollen from other inflorescences minimizing geitonogamy.

The hermaphrodite flowers are strongly protandrous (Figs. 3–5). During anther dehiscence inflorescences release clouds of pollen for several days. At the time of anther dehiscence the stigmas are barely visible (Fig. 3). After anther dehiscence they elongate (Fig. 4) but are not fully mature and receptive until 7–10 days later (Fig. 5). The lowermost hermaphrodite flowers are not receptive until 1–2 days after dehiscence of the last anthers on the inflorescence. In the hermaphrodite flowers, both autogamy and geitonogamy are prevented due to the temporal separation of the male and female functions.

After pollination the stigmas wither. If pollination does not occur, the stigmas may retain full turgidity indefinitely. The female spikelets that were covered to exclude pollen remained turgid for over three months until they were removed for weighing of the flowers.

The ovary of both types of flowers contains only one ovule. Ovaries with fertilized ovules barely increase in size during maturation of the embryo. A mature fruit is hardly different in diameter from an ovary with receptive stigmas. Mature fruits are usually purple in color and have a fleshy pericarp, whereas the immature flowers are green. The color and fleshiness of the fruits suggest the possibility of bird dispersal. Birds were not observed eating the fruits but the possibility does deserve further study. Fruits were observed to be dispersed from the spikelets by gravity alone.



FIGURES 2–5. Flowers of *Gunnera perpensa*.—2. Female flower with receptive stigmas.—3. Hermaphrodite flower just before anther dehiscence. The stigmas are barely visible above the sepal.—4. Hermaphrodite flower 2–3 days after anther dehiscence. Note elongation of stigmas.—5. Hermaphrodite flower with receptive stigmas, the staminal scars not visible. Scales = 1 mm.

TABLE 1. Fruit weights, flower number, gender values (G_i), and estimate of relative reproductive effort for *Gunnera perpensa*.

Plant Number	Floral Morph	Treatment	$\bar{x}$ Fruit Wt. of 50 Fruits (mg)	Flower Number	Floral Morph Ratios (female/ hermaph-rodite)	G_i	Male Reproductive Effort
1	♀	UT	20.2	15,272	2.22	0.43	0.98
	☿		24.2	6,868			
2	♀	UT	15.1	15,395	2.46	0.45	1.33*
	☿		13.7	6,259			
3	♀	UT	28.4	41,153	2.48	0.45	0.65
	☿		33.6	16,562			
4	♀	UT	16.6	36,199	3.11	0.49	0.88
	☿		26.4	11,658			
5	♀	UT	19.2	35,596	3.18	0.50	0.78
	☿		25.3	11,165			
6	♀	UT	18.9	12,644	3.45	0.51	0.75
	☿		25.2	3,670			
7	♀	UT	23.1	21,043	3.80	0.53	0.60
	☿		25.6	5,530			
8	♀	UT	18.2	58,670	5.32	0.60	0.53
	☿		26.8	11,028			
9	♀	EU	21.7	34,435	—	—	—
10	♀	EU	23.3	11,505	—	—	—
11	♀	EU	16.9	6,008	—	—	—
12	♀	EU	22.0	20,460	—	—	—
13	♀	EU	27.9	19,256	—	—	—
14	♀	EU	18.9	15,783	—	—	—
15	♀	EU	20.0	35,624	—	—	—
16	♀	EU	28.8	25,209	—	—	—
17	♀	EB	7.8	11,816	—	—	—
18	♀	EB	6.6	15,728	—	—	—
19	♀	EB	9.6	14,535	—	—	—
20	♀	EB	15.9	9,898	—	—	—
21	♀ + ☿	UB	10.8	50,716	—	—	—
22	♀ + ☿	UB	8.9	18,464	—	—	—
23	♀ + ☿	UB	12.6	14,110	—	—	—
24	♀ + ☿	UB	21.2	29,935	—	—	—

* See p. 243 of text for explanation of this value.

Flower number and floral morph ratios. Values for total flower number and floral morph ratios in marked, UT inflorescences are presented in Table 1. Inflorescences of *G. perpensa* produce enormous numbers of flowers ranging from approximately 14,000 to nearly 70,000. Although the lengths of the inflorescences were not quantified, there was a positive correlation between spike length and flower number.

In the eight inflorescences sampled, the number of female flowers far surpassed the number of hermaphrodites. The ratio of female to hermaphrodite flowers ranges from 2.22 to 5.32 with a mean of 3.25 (Table 1). There is no clear relationship between the total number of flowers on an inflorescence and the floral morph ratio. Thus a smaller inflorescence does not necessarily have a lower female/hermaphrodite ratio than does a larger one.

In the only other published study that provides flower ratios in gymonoecious taxa, Lloyd (1972a) recorded female/hermaphrodite ratios of approximately 0.10 and 1.86 for two species of *Cotula*. In contrast, Lowrey (1986) found a broad

range of ratios in five Hawaiian *Tetramolopium* species, from 1.5 to 10.3 with a mean of 5.2. Again there is a great deal of variation from small to large percentage of females, but in the small data sample available, gynomonoecious plants tend to have strongly female-biased flower ratios.

Fruit weights as a measure of fruit set and female reproductive effort. The mature fruit weights (from untreated inflorescences) of the female flowers were not significantly different ($t = 1.186$, $P > 0.05$) from those produced by the hermaphrodite flowers (Table 1). The reproductive effort per flower apparently is similar for the female function regardless of whether the flowers are female or hermaphrodite. This also indicates that both flower types are equally successful in producing mature fruits.

On the EU inflorescences, removal of the hermaphrodite flowers from an inflorescence before anthesis did not significantly change the mature fruit weights as compared to those in the untreated samples. The flowers apparently were successfully pollinated. Thus the female flowers do not need the presence of hermaphrodite flowers for successful pollination and fruit set, at least not in moderate or large-sized populations.

The fruit weights from inflorescences emasculated and covered, treatment EB, were significantly lower than the control fruits ($t = 3.949$, $P < 0.01$). This indicates that they were not pollinated and, as mentioned previously, all the flowers had turgid stigmas at the end of the three-month period, confirming the lack of pollination and fruit set. It would be valuable to artificially pollinate similarly treated inflorescences over increasing lengths of time to accurately determine the duration of stigma receptivity.

Finally, in untreated and covered inflorescences, treatment UB, fruits were also significantly lighter than the controls ($t = 2.448$, $P < 0.05$). It should be pointed out that inflorescence 18 in this treatment had weights well within the range of the untreated fruits. The presence and degree of self-compatibility cannot be accurately stated given the small sample size and the method of measurement. In spite of these shortcomings, the variation in fruit set on the plants in treatment UB does indicate geitonogamy as well as demonstrating a much lower parental success as opposed to outcrossing. Further studies on this point clearly are needed.

Functional gender and reproductive effort. The values calculated for functional gender give a different view of gender strategies in *G. perpensa* compared with that provided by floral morph ratios (Table 1). The relative femaleness varies from 43% to 60% with the low values corresponding to the lower flower ratios. Even at the very high percentage of female flowers, only 60% of a plant's fitness is transmitted through its ovules. The ratio at which both genders contribute equally is 3.12; in other words, there must be at least three times as many female flowers as hermaphrodites for the female gender to equal the male gender. This estimate of functional gender assumes a randomly outcrossing population. This may not always be the case since there is the possibility of geitonogamy, but until we have an accurate estimate of selfing it is best to treat the situation as an outcrossing one.

The values for the male reproductive effort show that the male input in a hermaphrodite flower is extremely high. At the lowest estimate of female gender (43%) the relative male reproductive effort approaches 1.0 (Table 1). Only at a female gender value of 60% does male reproductive effort (53%) approach equivalence to the female effort. Thus a major factor in the reproductive biology of *Gunnera perpensa* is the high cost of the male gender. This is not difficult to understand when the large amounts of pollen and large size of the anthers (Fig. 3) are considered. The reproductive effort for plant 2 is greater than 1.0, which is impossible since it is a relative value. This is due to the very low fruit weight that underestimates the female reproductive effort.

Pollen stainability, pollen/ovule ratios, and pollen storage products. The mean pollen stainability in *Gunnera perpensa* is 97.5% ± 0.11%. The mean pollen/ovule ratio is 17:386 ± 2:390. This P/O value places the species well within the range of values for other outcrossing wind-pollinated plants (Cruden, 1977; Pohl, 1937). In fact, considering the great number of hermaphrodite flowers produced on an inflorescence, one large inflorescence could produce nearly 300 million pollen grains, most of which would be fertile.

The results of the histochemical tests for the presence of lipids and/or starch also indicate wind pollination. The pollen tested positively for large amounts of starch in the protoplasm while only tiny amounts of lipids were found on the exine. It must be mentioned that the presence of starch also correlates with relatively large pollen grain size as shown for other plants by Baker & Baker (1979).

Discussion

The confirmation of gynomonoecy in the *Gunnera perpensa* populations investigated in this study is in direct conflict with most previous reports of polygamomonoecy in the species (Schindler, 1905; Boutique & Verdcourt, 1973; Mendes, 1978). It is probable that *G. perpensa* is gynomonoecious throughout its range in Africa, although this does need field confirmation. The species probably has been labeled mistakenly as polygamomonoecious due to the occasional presence of a few hermaphrodite flowers on the otherwise female spikelets and to the strong protandry of the hermaphrodite flowers, giving the impression of being male if observed at the beginning of anthesis. This confusion is not difficult to understand because all previous reports were contained in taxonomic descriptions undoubtedly derived from examination of herbarium specimens. Only field observations made over an extended period of time could have established the presence of the temporal separation of the different floral morph maturation sequences. This serves to emphasize the need for detailed field studies to adequately document temporal separation of sexual function.

The floral maturation sequence in *Gunnera* is actually a very interesting dichogamous system. It is a combination of both protogyny and protandry that effectively operates on the inflorescence level rather than at the flower level. In most other species where both phenomena co-occur, the plants are protandrous at the individual level and protogynous at the flower level or vice versa (Bawa & Beach, 1981). For example, in many andromonoecious Umbelliferae, the hermaphrodite flowers themselves may be protogynous but the inflorescences are protandrous due to earlier anthesis of female flowers; so from an individual point of view the plants are actually protandrous (Bell, 1971; Lindsey, 1982). As pointed out by Bawa & Beach (1981), it is the individual level phenomena that are evolutionarily and functionally important.

The adaptive function of dichogamy must be considered in conjunction with the sex expression and pollination system. Dichogamy traditionally has been assumed to function primarily as an outcrossing mechanism while limiting self-pollination. Cruden & Hermann-Parker (1977) labeled strongly dichogamous systems as being temporally dioecious, thus functioning to promote outcrossing. According to Bawa & Beach (1981), if this were its only function then both protandry and protogyny should be equal in function and equal in occurrence in plants regardless of taxonomic grouping. Since they are not, other hypotheses have been advanced to explain the differential occurrence. Several of these hypotheses accord well with the observations of dichogamy in *Gunnera*.

Bawa & Beach (1981) suggest that the evolution of protogyny is directly related to three aspects of the pollination biology. Their first hypothesis deals with the co-evolution of protogyny and specific insect pollinators (beetles and fig wasps), which has no application here. Their second hypothesis suggests that protogyny may have developed to prevent clogging of stigmas by self pollen. The occurrence of wind pollination in *Gunnera perpensa,* firmly established by the pollen/ovule ratios, pollen storage product tests, and the floral morphology data, could well cause pollen clogging if both the floral types mature together. There may be selection for protogyny, which may allow for some selfing if there is uncertainty of cross-pollination. The possibility for geitonogamy to occur in the female *Gunnera* flowers indicates that there may well have been some selection pressure for the fail-safe pollination mechanism offered by geitonogamy.

The presence of protandry can be explained both in terms of the limitation of selfing and, as in protogyny, prevention of stigma clogging by self pollen. Lloyd & Yates (1982) suggested the latter process as accounting for the evolution of protandry in *Wahlenbergia albomarginata.* Thus a combination of protandry and protogyny in *Gunnera* could function to prevent stigma clogging in the female flowers (via protogyny) and in the hermaphrodites (via protandry). Protogyny functions initially to prevent outcrossing and stigma clogging, but as the inflorescence matures it can also allow some geitonogamy to take place.

Dichogamy can function equally well in either monoecious or hermaphrodite inflorescences. Both forms of sex expression, as well as dichogamy, are known in other *Gunnera* species (Palkovic, 1978). The question of why gynomonoecy occurs in *G. perpensa* can only be answered by examining the functional gender and reproductive effort data.

The results show that gynomonoecy can function in *G. perpensa* to regulate the degree of femaleness and adjust the reproductive effort between the male and female genders. The degree of femaleness is mainly a consideration of breed-

ing behavior, that is, whether more of a plant's genes are transmitted through the ovules or through the pollen. In *Gunnera* the mean functional female gender value is 50%, showing equal genetic investment in both female and male functions. However, in a population the functional gender can vary 10–20%, with some inflorescences acting more as males and others as females.

The results of the functional gender calculations, while being important from the genetic aspect, do not alone provide a complete picture of the role of gynomonoecy. The values for relative reproductive effort provide the main key to understanding the functional significance of gynomonoecy in *Gunnera perpensa*. What emerges is that the cost of male reproductive structures is very high. The relative reproductive effort at the lower female gender values is largely male. Altering the gender balance with the addition of female flowers causes a sharp decrease in male effort, although even at the highest female gender estimate the reproductive effort only approaches 1 : 1. It must be borne in mind that thousands of female flowers are involved. Clearly in wind-pollinated plants with small fruits, the cost of producing large amounts of pollen and relatively large anthers exceeds the cost of producing fruits. The most economical method of increasing functional gender in such plants is through the addition of female flowers.

Lemen (1980) also found a positive correlation between reproductive effort and breeding system in wind-pollinated plants. The plants having very low male effort were strong inbreeders while the outcrossing taxa had nearly equal male and female reproductive efforts. If this relationship is generally applicable, then the relatively high male effort in *Gunnera perpensa* is indicative of outcrossing. Additionally, Lemen (1980) found that the highly outcrossed species he studied were self-incompatible. Our data do not conclusively rule out the presence of self-incompatibility but do suggest the plants are self-compatible to some extent. In *G. perpensa*, dichogamy rather than self-incompatibility acts to promote outcrossing in addition to its other functions. Also, due to the phylogenetic constraint of the flowers being uniovulate, the only way to increase ovule number is by increasing the number of female flowers (Lloyd, 1979; Webb, 1984).

One main feature of the reproductive system in *Gunnera* that needs study is what actually constitutes a population. If the populations investigated in this study are both clones with several hundred ramets each, then they represent only two genetically distinct individuals. This has important implications for the determination of breeding systems in all species in the genus. Although the flowers in an inflorescence may be outcrossed, genetically they may well be inbred if they receive pollen from a ramet neighbor. We intend to investigate the structure of the genetic neighborhood in *G. perpensa* in the near future. Much more research needs to be done to study the genetic implications of vegetative reproduction and sexual reproduction occurring simultaneously in a population.

In summary, our studies confirm several of the hypotheses advanced to explain the function of gynomonoecy. In a wind-pollinated plant, gynomoecy is an economical way of regulating functional gender because the male reproductive effort is so great. Adding large numbers of female flowers does not drastically change the gender ratio but the cost is considerably less than adding hermaphrodite flowers. Dichogamy may function to prevent stigma clogging in wind-pollination systems but also functions to promote outcrossing. Experiments are needed to test the actual importance of stigma clogging. The occurrence of a diverse range of sex expressions in *Gunnera* offers excellent possibilities for studies on the evolution of different sexual systems such as monoecy and dioecy. *Gunnera* is a particularly good potential subject for such studies since there are documented cases of hybridization between species with different sexual systems (Palkovic, 1978). It would be most interesting to investigate the reproductive biology of other gynomonoecious species of *Gunnera* (Palkovic, 1978) to see if they give similar results to *G. perpensa*.

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REPRODUCTIVE ECOLOGY OF TWO ECOTYPES OF *THEMEDA TRIANDRA* FORSK. (GRAMINEAE: ANDROPOGONEAE)

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Abstract

Themeda triandra, an important component of African grasslands and open woodlands, comprises several more or less distinct morphological, cytological, and ecological races. The present study on flowering phenology, fruit and pollen dispersal, pollination biology, and reproductive success has provided baseline data for two geographically closely sympatric, morphologically and ecologically distinct races. *Themeda triandra* is andromonoecious, with a high preponderance of male florets. Anthers of male spikelets produce considerably more pollen than anthers of hermaphrodite spikelets and all florets of both ecotypes produce pollen of low viability. Pollen density is rather low, even close to a stand. Hermaphrodite florets open first but self pollination seems to be ineffective. If pollination is not effective on the first day of anthesis, the style continues elongating and the stigma may remain receptive for up to 10 days. Anthesis of the male florets usually begins on the third to fifth day after the hermaphrodite floret opens. Opening of these florets is staggered, continuing for a number of days. Marked differences were found in duration of receptivity of stigmas between synchronously flowering individuals of the ecotypes. Seed set was significantly higher for one ecotype than for the other, but no statistically significant differences in seed set of dense or sparse stands were found. Reproductive success for bagged or totally isolated spikelets was similar to the lowest values found in open pollinated plants. Fruit dispersal by animals is responsible for long-distance dispersal, while wind dispersal seldom results in seeds being dispersed further than twice the canopy diameter. This phenomenon is responsible for the clumped distribution in many grasslands and, with the leptokurtic pollen distribution and apparently obligate pollination, suggests that clumping is important for successful reproduction in spite of widespread agamospermy in the species.

Résumé

Themeda triandra est un composant important des praires et des bois ouverts d'Afrique et comprise un nombre de races morphologiques, cytologiques et écologiques plus ou moins distinctes. Cette étude porte sur deux races très proches géographiquement et qui sont distinctes morphologiquement et écologiquement, et a pour but d'étudier les caracteristiques de la biologie reproductrice. *Themeda triandra* a des inflorescences paniculées dans lesquelles la partie fonctionnelle consiste en un ou plusieurs spicules hermaphrodites associés à un certain nombre de spicules ayant des fleurs mâles. La plante est donc andromonoïque avec une prédominance importante de fleurs mâles. Les anthères des spicules mâles produisent deux fois plus de pollen que celles des spicules hermaphrodites et toutes les fleurs des deux écotypes produisent du pollen à la viabilité assez uniformement basse. Ceci, ajouté aux courtes distances parcourues par la plupart des pollens, produit une densité sensiblement modifiée de pollens viables et des petites aires de pollinisation. Les fleurs hermaphrodites sont les premières à s'ouvrir et bien que les anthères s'ouvrent en même temps que les stigmates sont receptives, l'auto-pollinisation ne semble pas être efficace. En cas de pollinisation le premier jour après l'anthèse, le style se fane dans la soirée, mais lorsqu'il n'y a pas de pollinisation le style continue à s'allonger et le stigmate peut rester receptif pendant dix jours. L'anthèse des fleurs mâles commence 3–5 jours après que la fleur hermaphrodite s'est ouverte et est échelonnée sur plusieurs jours. Des différences statistiques significatives ont été trouvées quant à la durée de receptivité des stigmates à la fois entre des individus des écotypes qui fleurissent en même temps et entre des individus d'un écotype qui fleurissent plus tôt et plus tard. Les plantes de populations denses ont une receptivité des stigmates considérablement plus courte que des plantes isolées ou celles de populations éparses. La fécondité était plus élevée pour l'un des écotypes, mais il n'y avait pas de différences statistiques notables entre des populations denses ou éparses. La dispersion des fruits est faite par les animaux ou le vent. Les animaux dispersent les fruits sur des longues distances tandis que le vent disperse rarement les graines sur une distance deux fois plus grande que le diamètre de la voûte. Ce phénomène est clairement la cause de la dispersion groupée de *Themeda triandra* que l'on note dans de nombreuses prairies et si l'on ajoute à cela la distribution leptokurtique du pollen et l'échec apparent de l'auto-pollinisation il semble que le re-groupement soit important pour une bonne reproduction malgré une agamospermie répandue dans toute l'espèce.

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Themeda triandra is a widespread, perennial grass species occurring throughout Africa and extending through the Middle East to Asia Minor. In southern Africa the species occurs in most vegetation types [e.g., it is at least present in 52 of the 73 veld types recognized by Acocks (1975)]. Considering the geographical and ecological diversity alone, it is not surprising that the species shows tremendous morphological variability. This variability is reflected taxonomically, with many races having been recognized in the past (Clayton & Renvoize, 1982). In southern Africa at least four of these races are more or less distinct, differing in habit, morphology, chromosome number, and habitat. In some parts of the highveld of South Africa two distinctive forms may be found growing close together, and in some sites they are fully sympatric. Some geographical and ecological separation has been found for southern African cytological races (Gluckmann, 1951) as well as fairly clear-cut geographical separation between cytological races of *T. australis* in Australia (Hayman, 1960). In the central Witwatersrand area of South Africa, by contrast, cytological and morphological races are found growing within a few meters of one another, and in some places populations are intermixed. Clearly, such situations pose interesting questions concerning gene flow, the adaptive significance of infraspecific variation, and the nature of species.

As a starting point in a program of research on population and evolutionary biology of grasses, the work reported here had three major objectives: 1) To investigate flowering behavior of field populations. This would show whether the potential for genetic exchange was present or whether temporal isolation of the ecotypes occurred. In addition, the potential for autogamy and geitonogamy could be judged. 2) To investigate pollen and seed dispersal as a baseline for studies on genetic neighborhoods. The often patchy distribution of grass species in subtropical grasslands suggests small genetic neighborhoods, and the existence of sympatric/parapatric races of *Themeda triandra* provides an excellent system for studying this aspect of population structure. 3) To determine pollen viability and seed set and the influence of pollination on seed set. Since *Themeda triandra* is facultatively agamospermic, the role of pollination in reproduction needs investigation. Obviously, pollen and seed viability are central to any study of reproductive biology.

Materials and Methods

Study Site

Populations of the two forms (called ecotypes here) growing on an ungrazed area of land near Johannesburg, South Africa, were chosen for detailed study during the 1984/1985 flowering season. The study area comprises a dry hillside and a moist bottomland. There is some spatial separation of ecotypes, with the glabrous blue form distributed fairly evenly on the hillside and the hispid green form being almost exclusively confined to the bottomland, where it forms dense patches with some isolated plants away from the patches.

Methods

A sample of 16 plants (eight of each ecotype) were transplanted into pots in a garden and were used in testing for geitonogamy/autogamy. Observations were made of flowering phenology of both ecotypes from the time flowering commenced in October 1984 to the end of the major flowering period in December. Florets of plants of both ecotypes were marked as they opened and the course of anthesis was followed until fruit was shed. Duration of stigma receptivity and patterns of anthesis of associated male florets (see below) were recorded for marked spikelets. Caryopses collected from marked plants were scored for formation of seed.

Stigma receptivity was tested using hydrogen peroxide—receptive and damaged sites on stigmas and styles were indicated by rapid evolution of oxygen bubbles. A preliminary series of tests showed that stigmas remained receptive and styles turgid if kept moist, even when removed from the plant for up to 24 hours. Conversely, stigma receptivity was lost as soon as style branches began to wither. Stigma receptivity could therefore be determined nondestructively in the field by noting whether styles were turgid or wilted.

Pollen viability was inferred from results of staining pollen with cotton blue in lactophenol (Gurr, 1965). Pollen from single anthers from 36 plants of each ecotype—both hermaphrodite and male—were examined. Since undehisced anthers could be readily obtained and stored for a few hours in a saturated atmosphere in small vials, it was easy to spread the contents of an anther on a single slide with minimal loss of pollen. Counts were made on these slides, taking a sample of 200 fields of view at 150× magnification.

Grains with well-stained cytoplasm and which were not deformed were considered to be viable while unstained, weakly stained, or deformed grains were taken as being nonviable. In addition to determining stainability, these counts were used as a means of estimating numbers of pollen grains per anther. A check was made on these results using a hemocytometer, and since there was close agreement by both methods, numbers were determined by the former.

Pollen dispersal distances were estimated in two ways: quite frequently pollen was seen to be shed soon after an anther dehisced, and the distance the pollen cloud traveled could be measured directly. Measurements could be made in this way on only four days and for a small number of observations. In addition, small (50 cm long × 12 cm wide) strips of clear adhesive tape were placed within clumps and at different distances from isolated clumps of plants prior to anthesis. Each strip was curled into a cylinder around the supports, since rods are supposed to give better sampling efficiency than flat surfaces such as glass slides (Brun & Mergler, 1953, quoted by Player, 1979). These were collected after all florets had shed pollen for the day, placed on microscope slides, and subsequently viewed. In this preliminary survey, pollen dispersal was assessed on five days at the height of the flowering period using a total of 63 pollen collectors. Twenty collectors were used for the blue ecotype and 43 for the green ecotype. Unequal samples were chosen deliberately because of the greater diversity (clumped, patchily scattered, and widely separated, single plants) of the green ecotype. Pollen counts were made on these collectors, giving some measure of quantities of airborne grass pollen. A major problem associated with this method of assessing pollen dispersion is that all grass pollen appears very similar, and hence identification of the pollen source can be highly uncertain. This difficulty was somewhat alleviated by there being few other grass species flowering during this study, the almost monospecific nature of stands of *Themeda triandra*, and the fact that some of the other grass species flowering at the same time shed pollen later in the day than did *T. triandra*. Notwithstanding these fortunate circumstances, pollen collectors were not placed more than 2 m away from *T. triandra* stands, so most pollen might be expected to have come from the "target" stand.

Reproductive success was measured by proportions of spikelets that contained a well-developed seed as compared with those with none or aborted seed. Since small numbers of good seeds were obtained and germination trials were also required, only a very small subsample was tested for viability using tetrazolium salt (Porter et al., 1947). All seeds from 10 well-developed fruits stained when treated with tetrazolium after inbibition, so the results of visual assessment alone were used. Samples were obtained from open pollinated, clumped and isolated plants in the field, and from cultivated plants kept isolated from all sources of *Themeda triandra* pollen. In addition, a small number of spikelets were bagged using multiple layers of nylon stocking material. In trials at the beginning of the study it was found that although emasculation of the hermaphrodite floret had no adverse effect on seed formation, removal of the six male florets associated with each hermaphrodite often led to abortion of the entire spikelet. Thus we have not been able to conclusively distinguish geitonogamy from autogamy.

Propagule dispersal distances were determined in two ways. Some awns of hermaphrodite florets were marked with a small spot of brightly colored nail varnish and then the distance each had been carried by wind or water after being shed was measured. The second method was used for isolated plants and consisted of collecting all propagules found in a number of 10 cm wide belts radiating outwards from the tuft and measuring the distance from the parent tuft. Due to the dense nature of surrounding vegetation in the bottomland habitat, fruit dispersal distances were assessed only for the blue ecotype.

Results

Morphology

The inflorescence of *Themeda triandra* is a leafy false panicle borne on a lax culm. There are from one (or two) to six or more tiers of partial inflorescences, each subtended by a leaf or spathe and consisting of a number of spikelets enclosed within a spatheole. This comprises the functional unit of the inflorescence and has one or more hermaphrodite spikelets. Each hermaphrodite spikelet is associated with four sessile spikelets that form an involucrelike structure around the hermaphrodite spikelet and a short rachilla. The rachilla bears two pedicellate spikelets (in all plants examined), each of which has one male floret. The involucral and hermaphrodite spikelets each have a single functional floret. Plants

TABLE 1. Anthesis phenology for two ecotypes of *Themeda triandra*.

Days from Opening of Hermaphrodite Floret	Numbers of Florets Open			
	Blue Ecotype		Green Ecotype	
	Sessile N = 155	Pedicelled N = 34	Sessile N = 352	Pedicelled N = 88
1	0	0	9	0
2	9	1	0	1
3	10	2	5	0
4	16	5	18	0
5	30	36	65	12
6	36	7	71	20
7	26	4	71	4
8	11	9	36	14
9	12	2	16	2
10	0	0	18	10
11	5	2	11	4
12	0	0	8	0
13	0	0	2	0
14	0	0	24	9
15	0	0	4	1
16	0	0	0	0
17	0	0	0	0
19	0	0	0	0
20	0	0	0	0

are therefore andromonoecious with a predominance of male florets per functional unit, and hence per plant, of 6 : 1 (see below for pollen : ovule ratios).

FLOWERING PHENOLOGY

The flowering of a plant or even a large inflorescence extended over a long period; some inflorescences flowered intermittently from early October until February, but showed no consistent pattern of anthesis of functional units. By contrast, anthesis of the functional units followed a reasonably clear succession. Both ecotypes flowered at the same time of year. Individuals of both forms in wetter microsites flowered later than those in drier sites.

As in the case of season of flowering, both the blue and green ecotypes followed the same phenological sequences and duration of phases for flowering in the functional units. Anthesis of a functional unit began with the opening of the hermaphrodite floret. Anthers and style branches were exserted simultaneously, and stigmas were receptive on the same day and at the same general times as pollen was being shed by the anthers of the spikelet. The lodicules lost turgidity a few hours after anthesis and the lemmas closed. Pollen was shed by mid morning at the latest but styles remained turgid and stigmas receptive for varying periods of time (see below). Male florets opened sequentially, usually one at a time per functional unit, after opening of the hermaphrodite. The first male florets to open were the sessile, involucral ones. In a few cases (9 of 358 florets of the green ecotype only) sessile male florets opened on the same day as the hermaphrodite. Most involucral florets opened from the fourth or fifth day after anthesis of the hermaphrodite. Maximum frequency of sessile male floret opening was from day 5 through day 8 from first anthesis of the unit as a whole (Table 1). Involucral males continued opening up to 15 days from first anthesis. The pedicellate florets showed a similar pattern of anthesis, although the earliest recorded opening of a pedicellate male floret was one day after anthesis of the functional unit and peak opening extended from day 5 through day 10 after opening. As with involucral florets, opening continued for some time (up to 15 days) after first anthesis of a functional unit. In most cases, involucral and pedicellate florets opened on different days, although such temporal separation was far from absolute.

For both ecotypes and for anthers of male and hermaphrodite florets, pollen was shed early, never before sunrise but often before plants were actually in sun. Flowers thus began opening anytime from 5:45 A.M. on fine midsummer mornings through to as late as 7:30 A.M. on overcast or wet mornings. No correspondence was found between temperature and time of flower opening, but anther dehiscence and duration of shedding of pollen was influenced by both temperature and relative humidity (RH). Under warm and dry conditions anthers dehisced within 5–10 minutes of being exserted, but when conditions were cool and moist dehiscence could be delayed for 75–90 minutes after florets opened. Relative humidity seemed to play an important role in determining when dehiscence occurred: generally dehiscence began when RH had dropped to about 80% [mean ($\bar{x}$) = 77.5%, standard deviation (s.d.) = 17.24% for 25 days], although some anthers began dehiscing at over 90% RH, and on one morning shedding occurred at a relative humidity of 100%.

The time taken for an anther to empty completely ranged from 2 to 30 minutes. Slowest rates occurred when humidity was high, and the

most rapid (2 minutes from the pore opening to complete emptying) was observed on a dry, hot morning. Shedding from a plant was more extended than this, with sheltered florets and plants in moist microhabitats taking up to 2 hours before all florets had shed all pollen. Notwithstanding this variability, most plants had all exserted anthers empty by about 8:30 A.M., and no plants were found with pollen in dehisced anthers after 11:30 A.M.

POLLEN DISPERSAL

Direct measurement of the distances to which pollen drifted immediately on being shed suggested that the majority of pollen grains traveled only a short distance from the parent plant ($\bar{x}$ = 0.684 m; s.d. = 0.5152; range 0.100–1.9 m for 19 observations). Furthermore, there was no correlation with wind velocity ($r^2 = 0.0327$ for wind velocities from 0.25 to 1.05 m per second). These results represented minimum distances, since direct observation was only possible early in the morning, as anthers first dehisced, when wind was light and pollen would be expected to be heavy due to the high ambient humidity (Faegri & van der Pijl, 1979). Rate of fall under calm conditions was noted as 11 and 14 cm per second on the only two occasions of dead calm when pollen shedding was observed.

Data from the pollen collectors did not allow much refinement of these observations, in part due to the high variability of data from the smallest sample, and in part because pollen collectors could not be placed far enough away from stands of *Themeda triandra* to test for a decrease in pollen density over long distances. As the data show (Table 2), amounts of pollen trapped per cm^2 vary greatly from site to site and within sites. Pollen collectors within clumps of the blue ecotype showed low numbers of pollen grains at the centers of clumps and higher numbers of captured grains at stations 1 m from the center than at any other stations. This contrasted with the pattern shown by the green biotype, where there was a decrease from the center to 2 m from the nearest plant.

Statistical analyses of these data indicated that none of the differences between means found in this study were significant. However, a number of pairs of means were almost significantly different, suggesting that a larger sample might detect differences.

Irrespective of the shape of the pollen frequency curves, even close to a source of pollen, only a few pollen grains would be expected to contact a given stigma on a particular day. In addition, the high variability in pollen frequency on the collectors indicated that pollen was distributed very unevenly over a stand or at a distance from the stand. In contrast with this pattern for generalized dispersal, direct observations of anther shedding showed that the probability of selfing was high, particularly for florets low on a culm.

TABLE 2. Pollen dispersal ranges and numbers of grains captured on adhesive tape cylinders.

Ecotype	Distance from Center (m)	Sample Size	Numbers of Pollen Grains (per square centimeter)	
			Mean	s.d.
Blue	0	14	68.1	78.34
Green	0	20	96.9	110.58
Blue	1	3	199.6	183.49
Green	1	15	98.3	77.99
Blue	2	3	70.9	36.11
Green	2	15	61.6	41.71

POLLEN VIABILITY AND QUANTITY

Viability of pollen from anthers of hermaphrodite florets of blue ecotype plants averaged 64.5% viability (s.d. = 20.81%; range = 22.8–96.1%) while that from anthers of male florets averaged 73.5% (s.d. = 21.95%; range = 27.4–95.5%) and these means were not significantly different from one another ($P > 0.05$).

Pollen from the green ecotype showed less variation in viability, although male and hermaphrodite florets produced significantly lower percentages of viable pollen than did the corresponding anthers of blue ecotype plants (Table 3). Male florets averaged 53.6% viability (s.d. = 7.33%; range = 40.7–65.3%) while hermaphrodite florets produced an average of 48.3% viable pollen (s.d. = 8.01%; range = 30.3–62.2%).

The high variability in the data for the blue ecotype indicated that pollination success was likely to vary within stands of the population and that pollination contribution was not equally distributed amongst all plants. By contrast, and despite significantly lower overall values, pollen viability for individuals of the green ecotype was rather uniform.

Total pollen production per anther showed high variation for both floret types. In both ecotypes

TABLE 3. Pollen viability from plants of blue and green ecotypes of *Themeda triandra*.

	BM	BH	GM	GH
Mean viability (%)	73.5	64.5	53.6	48.3
Differences between means (±s.e.)				
BM	—	9.0 ±6.16	19.9 ±4.47	25.1 ±5.57
BH	NS	—	10.86 ±2.09	16.2 ±3.92
GM	***	***	—	5.3 ±2.59
GH	***	***	Just NS	—

BM = blue male; BH = blue hermaphrodite; GM = green male; GH = green hermaphrodite; NS = $P > 0.05$; Just NS = $0.1 > P > 0.05$; *** = $P < 0.001$ on two-tail t-test.

the variation in numbers of grains per floret was correspondingly high. For the blue ecotype, single anthers of male florets produced between 2,453 and 12,792 grains ($\bar{x}$ = 7,461.3; s.d. = 2,311.69) and hermaphrodite floret anthers had from 923 to 4,490 ($\bar{x}$ = 2,493.6; s.d. = 1,323.64) grains. Male florets therefore produced an average of 22,383.9 grains and hermaphrodites produced 7,480.8 grains.

The green ecotype produced significantly less grains (Table 4) in the corresponding anthers than did the blue ecotype. Anthers of male florets of the green plants produced between 1,346 and 6,903 ($\bar{x}$ = 4,516.0; s.d. = 1,375.51) grains, and hermaphrodite floret anthers produced 852 to 3,690 ($\bar{x}$ = 2,102.6; s.d. = 929.87) grains. From these data, each male floret produces an average of 13,548.0 pollen grains and each hermaphrodite 6,307.8 grains.

POLLEN : OVULE RATIO

Data for pollen grain numbers indicates that the blue biotype had a pollen to ovule ratio per functional unit of 141,784.2 : 1. Similarly, plants of the green ecotype had average pollen : ovule ratios of 87,595.8 : 1. Even allowing for the modest pollen viability, these data represent very high resource allocation to male effort. All values are far in excess of those reported by Cruden (1977) for chasmogamous grasses.

STIGMA RECEPTIVITY

Stigmas of at least a few plants of each ecotype remained receptive for extended periods (Table 5), 11 days for a single floret of the blue ecotype and 10 days for a floret on an isolated plant of the green ecotype. Thus in regard to absolute duration of receptivity, the two ecotypes appeared similar. Closer inspection of the data, however, showed marked differences between forms. Curves were fitted by the method of least squares to the frequency distributions of stigma receptivity time.

In the case of the blue ecotype, the appropriate equation for retention of receptivity was: $Y = 234.07 (\exp 0.444X)$, where Y is the percentage of stigmas remaining receptive and X is the number of days after anthesis. The line given by this equation gave a good fit to the observed frequency distribution [coefficient of regression (r^2) = 0.9476; $P < 0.1\%$ for 10 degrees of freedom (d.f.)]. The half-life of a stigma (i.e., period at which 50% of florets opening on a particular day were still receptive) could be obtained from this equation, giving a half-life of 3.32 days.

For the green ecotype, the best fit was given by the equation: $Y = 12.46–2.44(\log X)$ (r^2 = 0.9650; $P < 0.1\%$ with 9 d.f.). From this line the half-life of a stigma from the green ecotype populations was 2.77 days.

SEED SET AS A MEASURE OF REPRODUCTIVE SUCCESS

Proportion of florets which set seed. Overall seed set was poor, with best results being obtained for plants in the field as opposed to cultivated plants (Table 6). Seed set was less than 50% for both ecotypes in all sites.

The data from field-collected seed as well as seed from cultivated plants were compared by t-tests (Table 6). The percentage seed set varied widely for both ecotypes and under different conditions.

TABLE 4. Pollen loads of anthers of male and hermaphrodite florets of two ecotypes of *Themeda triandra.*

	Blue Male	Blue Hermaphrodite	Green Male	Green Hermaphrodite
Mean no. of pollen grains per anther	7,461.3	2,493.6	4,682.8	2,342.3
Differences between means (±s.e.)				
Blue male	—	4,967.7 ±615.61	2,778.5 ±599.93	5,119.0 ±608.07
Blue hermaphrodite	***	—	2,189.2 ±407.91	151.3 ±393.13
Green male	***	***	—	2,340.5 ±366.53
Green hermaphrodite	***	NS	***	—

*** = $P < 0.001$; NS = no significant difference between means.

Of particular significance, however, were the data for isolated and bagged plants under cultivation. In both ecotypes, there was no significant difference between open pollinated plants and plants with bagged spikelets. In both cases, cultivated, isolated, or bagged plants produced slightly less seed than did open pollinated, cultivated plants, although these differences were not significant. The only differences that were significant were either between ecotypes or between cultivated and field-grown plants. In the case of the blue ecotype, cultivated, open pollinated plants produced less seed ($P < 0.05$; 11 d.f.) than isolated field-grown plants and less ($P < 0.01$; 24 d.f.) seed than clumped plants in the field. For the green ecotype, cultivated, open pollinated plants produced less seed ($P < 0.01$; 15 d.f.) than isolated plants in the field.

The ecotypes differed significantly from one another in seed set, with the green form showing higher reproductive success than the blue under a number of situations. It is noteworthy that even isolated green plants produced more seed ($P < 0.01$; 29 d.f.) than clumped blue plants, refuting the idea that pollination effects due to spatial population structure alone were responsible for poor reproductive success in the blue ecotype. Isolated plants of the blue ecotype showed significantly higher reproductive success ($P < 0.01$; 27 d.f.) than clumped blue plants and were not significantly different from field-grown green plants, perhaps suggesting competition for resources.

Seed mass. Comparisons of mean seed masses for different ecotypes and situations (Table 7) indicate that isolated plants of the blue ecotype produced heavier propagules than open pollinated plants from clumps ($P < 0.01$ with 66 d.f.), while propagules from isolated or bagged green ecotype plants were not different from those of plants in dense stands. There was no significant difference between propagule mass for green and blue plants in spite of differences in awn lengths (see below).

Interpretation of these results is difficult at present. Resource limitation cannot be considered to be the factor producing heavier propagules in the bagged or isolated plants grown in the garden, since these plants also produced heavier propagules than did plants B1–B6, which were transplanted from the same stands in the field and grown under identical conditions. Furthermore, blue plants from clumped populations in the field also had heavier propagules than the

TABLE 5. Percentage frequencies of stigmas still receptive at various times after anthesis of hermaphrodite florets of green and blue ecotypes of *Themeda triandra.*

	Days from Opening											
Ecotype	1	2	3	4	5	6	7	8	9	10	11	12
Blue	29.4	25.4	21.4	10.7	7.1	4.0	1.0	0.4	0.4	0.1	0	0
Green	43.7	24.0	12.6	8.9	4.5	2.8	2.5	0.8	0.2	0	0	0

TABLE 6. Reproductive success (numbers of fruits formed as percentage of florets marked) for blue and green ecotypes of *Themeda triandra*.

	Ecotype/Habitat							
	BCF	BCC	BIF	BIC	GCF	GCC	GIF	GIC
Mean % fruit set	22.1	12.3	44.8	18.0	40.0	22.0	44.5	33.3
Differences between means (±s.e.)								
BCF	—	9.8 ±3.29	22.7 ±6.66	3.9 ±4.42	17.9 ±3.60	0.1 ±4.36	22.4 ±3.96	0.2 ±3.94
BCC	**	—	32.5 ±13.27	5.7 ±6.82	27.7 ±6.85	9.7 ±7.47	32.2 ±4.04	21.0 ±5.20
BIF	***	*	—	26.8 ±15.73	4.8 ±7.95	22.8 ±12.44	0.3 ±10.6	11.5 ±13.77
BIC	NS	NS	NS	—	22.0 ±7.41	4.0 ±9.21	26.5 ±8.32	15.3 ±8.26
GCF	***	***	NS	**	—	18.0 ±6.60	4.5 ±5.71	6.7 ±7.15
GCC	NS	NS	NS	NS	Just NS	—	22.5 ±7.69	13.3 ±7.69
GIC	***	***	NS	**	NS	**	—	22.7 ±7.69
GIF	**	**	NS	NS	NS	NS	NS	—

BCF = blue ecotype, clumped, field grown. BCC = blue ecotype, clumped, cultivated. BIF = blue ecotype, isolated, field grown. BIC = blue ecotype, isolated/bagged, cultivated. GCF = green ecotype, clumped, field grown. GCC = green ecotype, clumped, cultivated. GIF = green ecotype, isolated, field grown. GIC = green ecotype, isolated/bagged, cultivated. *** = $P < 0.001$; ** = $P < 0.01$; * = $P < 0.05$; Just NS = $1.0 > P > 0.05$; NS = $P > 0.05$.

cultivated, outcrossing blue plants. It therefore seems that propagule mass is an indication of inherent variability of the blue ecotype or of some feature of the reproductive biology.

PROPAGULE DISPERSAL

Caryopses of *Themeda triandra* are shed enclosed by indurated lemmas. The fertile lemma has a long, hygroscopic awn, and the base of the floret has a long, pungent callus with staff ascending hairs. Awn lengths differed slightly for the two ecotypes, 30–50 mm long in the green form and 40–70 mm long in the blue ecotype. As in many andropogonoid grasses, dispersal in *T. triandra* is by abiotic and biotic agents. Since no animals were included in the study area, biotic dispersal was not observed.

Abiotic dispersal was by wind or water. Wind, by causing culms to whip back and forth, shook propagules from the inflorescence. The heavy propagules (see above) of *Themeda triandra* were not moved long distances by this agent (see Table 8). Maximum wind velocity when propagules were dispersed during the study was 5 m per second, and the maximum distance from the parent plant that a propagule moved under these conditions was 1.38 m. Water acted as a dispersal agent due to movements of the awns. The twisting of awns as they dried out after wetting by rain or dew often dislodged propagules, which then fell to the ground.

Both abiotic agents of dispersal thus produced highly leptokurtic distribution of seeds. In effect, dispersal radii were little greater than the height of the culm from which a propagule fell. Abiotic dispersal thus produces clumping of plants around the parent, and only when animals move through a stand will long-range dispersal occur.

DISCUSSION

Themeda triandra has been shown to be facultatively agamospermic (Brown & Emery, 1957). It would therefore be expected that allocation to male effort would be reduced or lost.

TABLE 7. Propagule mass from plants of green and blue ecotypes of *Themeda triandra*.

	Blue			Green	
	Isolated	Clumped	B1–B6	Isolated	Clumped
Mean mass (g)	0.0140	0.0082	0.0097	0.0119	0.0127
Differences between means (±s.e.)					
Blue					
Isolated	—	0.0058 ±4.47e − 4	0.0043 ±4.62e − 4	0.0021 ±5.68e − 4	0.0013 ±0.00218
Clumped	**	—	0.0015 ±3.88e − 4	0.0037 ±4.02e − 4	0.0045 ±0.00193
Green					
Isolated	***	***	**	—	0.0008 ±0.00298
Clumped	NS	NS	NS	NS	—

*** = $P < 0.001$; ** = $P < 0.01$; * = $P < 0.05$; NS = $0.1 > P > 0.05$.
Values for standard error given in scientific notation.

However, Connor (1979) indicated that most apomictic grasses are pseudogamous and thus pollination is required for reproduction, even though fertilization may not occur. The high investment in male florets and pollen clearly shows the significance of pollination in the ecotypes studied. Furthermore, the large amount of pollen produced suggests that at least the blue ecotype may indeed be outcrossing. The smaller amounts of pollen produced by the green ecotype suggest that this form may be developing increased dependence on agamospermy. The data on stigma receptivity duration is most important in this context. Observations that most plants of the green ecotype (which grew in dense stands) had receptive stigmas for only a short while and that only isolated plants of the green ecotype showed extended stigma receptivity, as well as the greater stigma half-life in the scattered plants of blue ecotype populations and the indication that pollen density dropped off rapidly with increasing distance from a stand, suggest that duration of stigma receptivity is an indication of pollination success. If this is so, clumping of green ecotype plants more than compensated for lower pollen production, and this indicates that clumping in general may be of advantage. This suggests that a balance between long- and short-distance seed dispersal and the ability to produce at least some seed even when plants are isolated would be favored. This is just what is found in *Themeda triandra*: specialization of the large propagules for animal dispersal plus reproduction (albeit at low levels) in bagged spikelets.

As Bawa & Beach (1981) pointed out, distinction has to be made between dichogamy at the flower and plant levels. Andromonoecy in *Themeda triandra* resulted in neither temporal nor spatial dichogamy. Nonetheless, the sequential opening of florets of a functional unit may be a response to the adverse affects of stigma clogging by self-pollen. Bawa & Beach (1981) suggested that protogyny should evolve under conditions where stigma clogging was prevalent. Although *T. triandra* is not protogynous, the production of pollen by hermaphrodite florets is far lower than that of male florets. Most pollen from a functional unit is shed after the stigma of that

TABLE 8. Frequency of occurrence of propagules at various distances from a parent plant. Data are for 466 propagules of the blue ecotype.

Distance (mm)	Frequency (%)
0–100	7.3
101–200	35.4
201–300	24.0
301–400	7.9
401–500	10.5
501–600	7.3
601–700	2.8
701–800	1.5
801–900	1.3
901–1,001	0.9
1,001–1,100	0.6
1,101–1,200	0.2
1,201–1,300	0.2
1,301–1,400	0.2

unit becomes nonreceptive, at least for plants in dense stands. In this sense, the staggered opening of florets might represent a balance between avoidance of clogging of stigmas and extended duration of pollen production even in plants with small inflorescences. Reduction of pollen output from hermaphrodite anthers may be a further means of reducing self-clogging of stigmas, or it may be due to resource constraints in the hermaphrodite floret. Under conditions of short stigma receptivity (less than two days), geitonogamous pollination would only be from florets of other functional units. Self pollination would also be possible since pollen shedding and stigma receptivity in the hermaphrodite floret is synchronous, but the small amounts of pollen in these anthers might be ineffectual. This situation held for the majority of plants of the green ecotype. However, plants of the blue ecotype mostly have hermaphrodite florets which remain receptive long enough for male florets of their own functional unit to shed pollen, greatly increasing the probability of self pollination. For the blue ecotype at least, there is correspondence between decline in stigma receptivity and the proportions of male florets of the same functional unit shedding pollen. By contrast, with the exception of a single plant that was far from any other flowering individuals, green ecotype plants showed maximum loss of receptivity before male florets of the same functional unit opened.

Reproductive success as measured by seed production was poor. However, the significant feature of the data collected for the ecotypes is that self pollination, whether from anthers of the hermaphrodite floret, from one of the six male florets in the functional unit, or from another functional unit on the same plant, was just as effective in initiating seed formation. The differences in propagule mass between blue and green ecotypes do not necessarily represent any differences in seed size, since the sterile appendages of the propagules (and particularly the awns) differ in size.

Gluckmann (1951) showed that the blue ecotype was tetraploid, $2n = 40$, and that the green ecotype was aneuploid with $2n = 52$. These cytological differences correlate with many observed morphological features (Gluckmann, 1951; Chippindall, 1955) and some of the reproductive biological features found in this study. Irrespective of the source of differences, or whether it is seeds or sterile parts that are enlarged, larger propagules represent increased reproductive investment.

Conclusion

This study has provided baseline data on seed and pollen production in closely adjacent populations of ecotypes of *Themeda triandra*. Pollen production and pollen : ovule ratios are high, suggesting outcrossing, at least as far as pollination is concerned. Although agamospermic seed production cannot be excluded, the data suggest that pollination is essential for seed production and that population density markedly influences pollination success. Even in dense stands, reproductive success is limited for both ecotypes. Conversely, even isolated or bagged plants produce seed, indicating the possibility of self pollination.

Themeda triandra expends appreciable energy on reproduction as indicated by the heavy propagules and high pollen production. The ecotypes differ in both of these features, with the blue form producing more pollen and heavier propagules than the green ecotype.

Data on pollen dispersal were inadequate to make any firm statements concerning pollen density at different distances. The data obtained suggested that pollen density dropped rapidly with increasing distance from its source, but larger samples are required for clear distinctions to be made. In contrast with pollen dispersal, data for abiotic seed transport showed marked clumping of seed around parent plants. It is suggested that a balance between abiotic short-range and biotic long-range dispersal of seed may be essential for adequate reproductive success in *Themeda triandra*.

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THE ASSOCIATION BETWEEN OIL-PRODUCING FLOWERS AND OIL-COLLECTING BEES IN THE DRAKENSBERG OF SOUTHERN AFRICA[1]

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ABSTRACT

Twelve *Diascia* species (Scrophulariaceae), each with flowers possessing a pair of spurs containing oil-secreting glands, have been found to be pollinated by oil-collecting bees in the genus *Rediviva* (Melittidae) in the Drakensberg of southern Africa. Variability in flower size and spur length among the *Diascia* species was quantified and shown to exceed the corresponding variability in foreleg length and overall size among the species of *Rediviva* pollinators. Species specificity among the pollinators was low. Only four different *Rediviva* species were collected and only two of these (*R. neliana* Cockerell and *R.* sp. nov. 1) are widespread and common pollinators of *Diascia*. *Rediviva neliana* pollinates nine *Diascia* species, while *R.* sp. nov. 1 pollinates six species. Some *Diascia* spp. are pollinated by more than one *Rediviva* species even in the same locality. In areas of sympatry between two or more *Diascia* species, one bee may visit more than one *Diascia* species even on a single foraging trip. In such cases interspecific pollen flow is minimized by differences among the species in stamen and stigma placement within the flower. Depending on the species, pollen is deposited on the head, sternum, or dorsal abdominal tergites of the visiting bee. All of the Drakensberg *Diascia* species are self-incompatible and therefore dependent on bees for pollination.

RÉSUMÉ

On s'est aperçu que 12 espèces de *Diascia* (Scrophulariacées), qui ont toutes des fleurs avec une paire de saillies contenant des glandes qui secrètent de l'huile, sont pollinisées par des abeilles du genre *Rediviva* (Mellitidae) dans le Drakensberg du sud de l'Afrique. Nous avons déterminé le taux de variabilité dans la taille des fleurs et la longueur des saillies pour les espèces de *Diascia* et on s'est apperçu qu'il dépassait le taux de variabilité correspondant pour la longueur de la patte antérieure et la taille globale parmi les espèces pollinisatrices de *Rediviva*. La spécificité des espèces parmi les pollinisateurs de *Diascia* est peu élevée. Seules quatre espèces différentes de *Rediviva* ont été récoltées et deux d'entre elles seulement (*R. neliana* Cockerell et *R.* sp. nov. 1) sont des pollinisateurs communs et répandus. *Rediviva neliana* pollinise neuf espèces de *Diascia* tandis que l'espèce *R.* sp. nov. 1 en pollinise six. Des espèces de *Diascia* sont pollinisées par plus d'une espèce de *Rediviva*, même dans en emplacement semblable. Dans des régions de sympatrie entre deux espèces ou plus de *Diascia*, une abeille peut se poser sur plus d'une espèce de *Diascia* en un seul voyage. En de telles occasions, le flux interspécifique de pollen est minimisé par les différences dans les espèces de l'emplacement des étamines et des stigmates. Selon l'espèce, les pollens sont déposés sur la tête, le sternum, ou les tergites dorsales ou abdominales de l'abeille. Toutes les espèces de *Diascia* du Drakensberg sont auto-incompatibles et dépendent donc des abeilles pour leur pollinisation.

The flowering plants have evolved a wide array of floral specializations to achieve pollen transfer among conspecifics. Most of these involve the production of a floral reward that promotes animal mediated pollen dispersal. Pollen and/or nectar are the most important of these, but there are a wide range of other substances that attract various specialized pollinators (Faegri & van der Pijl, 1979; Simpson & Neff, 1981, 1983; Armbruster, 1984). One of the most important of these for certain bee-pollinated plants is oil (Vogel, 1969, 1974, 1976, 1981, 1984; Simpson &

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Neff, 1981, 1983; Simpson et al., 1984; Neff & Simpson, 1981).

Plants in eight families have been recognized as having flowers that produce an oily material usually consisting of free fatty acids (C16–C20) (Siegler et al., 1978; Simpson et al., 1977, 1979; Cane et al., 1983) or glycerides with similar free fatty acids as constituents (Vogel, 1974; Steiner, unpubl.). This oil is secreted from patches of glandular trichomes (trichome elaiophores) on various parts of the flower or from larger floral glands in which the oil-secreting region is covered by a cuticle (epithelial elaiophores) as in the Malpighiaceae and Krameriaceae.

Floral oils appear to serve primarily a nutritional function as a constituent of the brood provisions (Simpson & Neff, 1981). However, Cane et al. (1983) have found that the oil collected by *Macropis* from *Lysimachia* (Primulaceae) is additionally utilized as part of the nest cell lining. Simpson & Neff (1983) speculate that the main advantage of oil over nectar, the usual substance that is mixed with pollen in the nest, is its greater energy content per unit weight than carbohydrates. All oil-collecting bees visit nectar flowers for their own sustenance and many supplement the pollen collected from oil flowers with pollen from other types of flowers (Vogel, 1974; Steiner, unpubl.).

Oil flowers and oil-collecting bees were initially known only from the New World (Vogel, 1969, 1974), but subsequent reports established their existence in Holarctic regions (Vogel, 1976) and in the Paleotropics (Africa and Borneo; Vogel, 1981). Recently they have been found in southern Africa as well (Whitehead et al., 1984; Hilliard & Burtt, 1984; Vogel, 1984; Manning & Brothers, 1986).

In the Neotropics and temperate South America, the oil-collecting bees are confined to four tribes in the Anthophoridae. In Old and New World north temperate regions, oil collecting is found in a single genus, *Macropus,* (Melittidae) (Vogel, 1976; Cane et al., 1983); in the Paleotropics oil is collected by *Ctenoplectra* (Ctenoplectridae) (Vogel, 1981), while in southern Africa oil collecting has been reported only for *Rediviva* (Melittidae) (Whitehead et al., 1984; Hilliard & Burtt, 1984; Vogel, 1984; Whitehead & Steiner, 1985a, 1985b; Manning & Brothers, 1986). *Ctenoplectra* also occurs in this region and probably collects oil here as well.

The manner in which the various types of oil-collecting bees collect oil reflects the manner in which the oil is presented by the flowers, but in all but *Tapinotaspis* (Tapinotaspoides) *tucumana* and *Ctenoplectra,* oil collection involves the use of the forelegs alone or in conjunction with the middle legs (Vogel, 1974, 1976, 1981; Neff & Simpson, 1981; Cane et al., 1983).

Many of the neotropical anthophorid oil collectors (most *Centris, Epicharis, Tetrapedia,* and *Paratetrapedia*) collect oil from epithelial elaiophores with scrapers formed from modified setae, but other genera (most *Tapinotaspis,* some *Centris, Chalepogenus,* et al.) collect oil from trichome elaiophores using dense pads of setae (Neff & Simpson, 1981; Vogel, 1974). *Macropis* and *Rediviva* are similar to the latter group with finely divided hairs and scalelike setae for collecting oil (Vogel, 1976, 1984; Michener, 1981; Whitehead et al., 1984; Steiner & Whitehead, unpubl.), while *Ctenoplectra* and *Tapinotaspis tucumana* have specialized oil-collecting hairs on the underside of the abdomen (Neff & Simpson, 1981; Vogel, 1981).

The presence of oil-collecting bees in southern Africa is a recent discovery (Whitehead et al., 1984; Vogel, 1984; Hilliard & Burtt, 1984) even though Vogel (1974) predicted their existence earlier after recognizing that two South African taxa, *Diascia* and *Bowkeria,* produced floral oils. Michener (1981) hypothesized that *Rediviva* spp. in southern Africa were oil-collecting bees, based on morphological similarities with the known oil-collecting bee *Macropus,* but he was apparently unaware of the existence of oil-secreting flowers. Although the association between oil-collecting bees and *Diascia* is now known, this knowledge is based on a limited amount of data. Whitehead et al. (1984) based their report on the pollination of *D. longicornis* by *R. longimanus* on three mornings of observation in the southwestern Cape; Manning (in Hilliard & Burtt, 1984) reported three visits by *Rediviva politissima* (Cockerell) (= *Rediviva neliana* Cockerell) to *Diascia anastrepta* during one hour of observation in the Drakensberg, while Vogel (1984) reported the association between *Rediviva emdeorum* and *Diascia longicornis* from a single bee specimen collected for him by U. Müller-Doblies (Vogel did not actually make any observations himself). Although Whitehead et al. and Vogel report different bees from the same *Diascia* species, this is due to a confusion in the taxonomy of *Diascia* section *Diascia.* They actually looked at different species of *Diascia,* neither of which was *D. longicornis* (Thunb.) Druce (Stei-

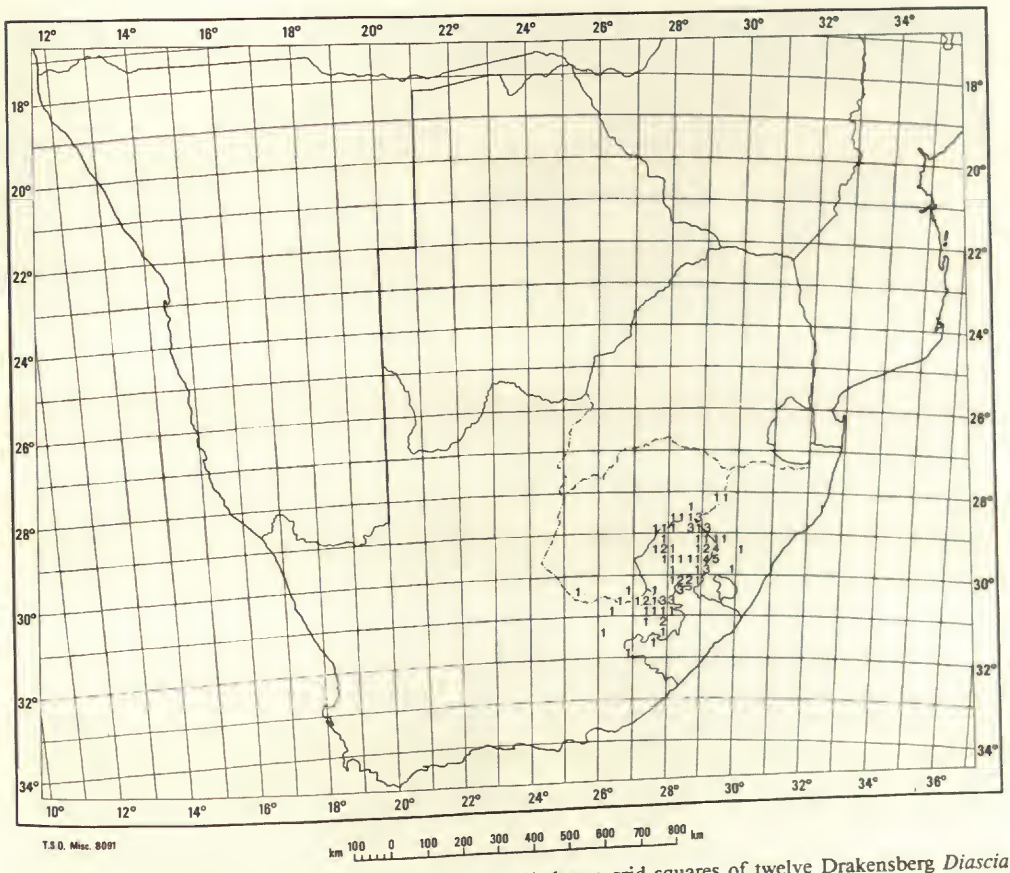

FIGURE 1. Distribution and species density within ¼ degree grid squares of twelve Drakensberg *Diascia* species in southern Africa.

ner, unpubl.). Recently Manning & Brothers (1986) reported floral visits by *R. politissima* (= *R. neliana*) to *Diascia anastrepta, D. cordata, D. integerrima,* and *D. barberae* as well as a single visit by *Rediviva* sp. to *D. purpurea.* They also provided the first observations of oil collection from *Bowkeria* and floral visits by *R. colorata* to a variety of nectar plants. They did not indicate the number of bees collected or the hours spent in observation (cf. Discussion).

The genus *Diascia* consists of about 50 species, 20 of which are perennials that occur primarily in the eastern parts of southern Africa. The largest concentration of perennial species (12 spp.) occurs in the Drakensberg. Hilliard & Burtt (1984) recognized 11 species from the Drakensberg, but our observations suggest that they have included two distinct taxa under the name *D. barberae* and, therefore, pending further study, we designate these as *D. barberae* and *D.* "*barberae.*" The species density and overall range of the Drakensberg *Diascia* species is presented in Figure 1 and is based on Hilliard & Burtt (1984) and our own observations.

Most *Diascia* species, whether annual or perennial, are characterized by two prominent spurs or sacs on the lower back surface of the flowers (Figs. 3–5). These spurs vary in size and shape, but all contain a patch of glandular trichomes near their tips that secrete oil (Vogel, 1974, 1984; Hilliard & Burtt, 1984; Steiner, unpubl.). A characteristic feature of flowers of *Diascia* section Racemosae is the presence of a yellow translucent area at the base of the upper corolla lobes known as the window (Hilliard & Burtt, 1984). Preliminary observations suggest that this functions as an orientation cue for visiting bees (Steiner, unpubl.).

In their recent revision of *Diascia* section Racemosae, Hilliard & Burtt (1984) suggested that

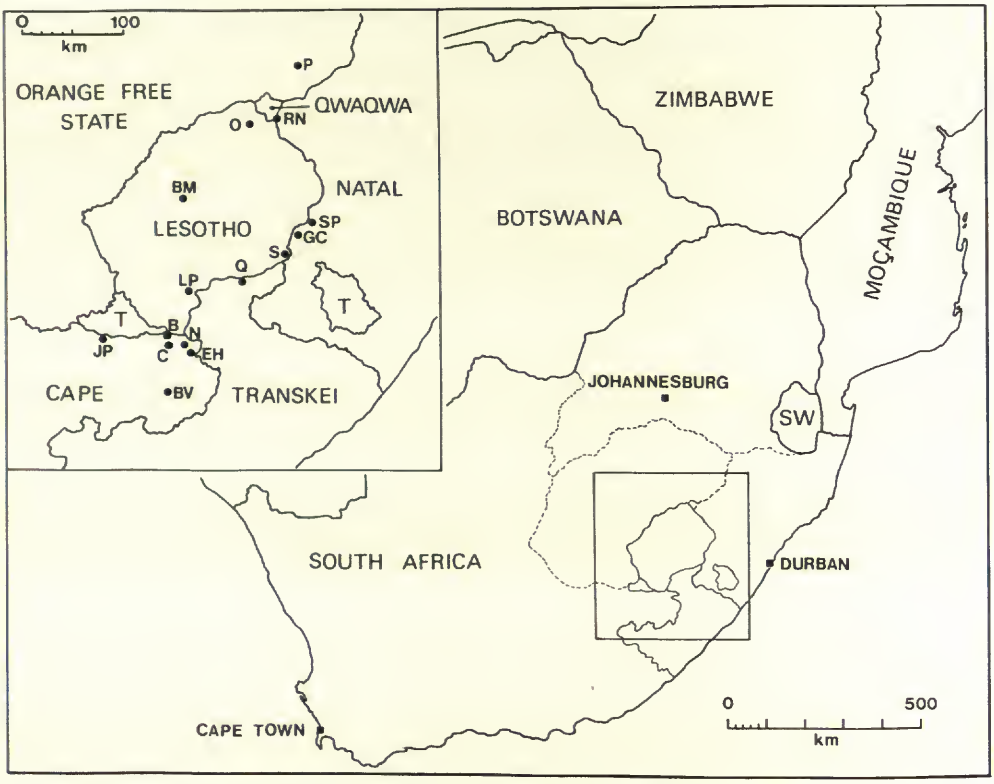

FIGURE 2. Collecting localities of bees in southern Africa. P = Platberg, RN = Royal Natal National Park, O = Oxbow, BM = Blue Mountain Pass, LP = Lebelonyane Pass, Q = near Qachas Nek but in Transkei, S = Sehlabathbe, GC = Garden Castle, SP = Sani Pass, JP = Joubert's Pass, B = Ben Macdhui, N = Naudesnek, C = Carlisleshoek, EH = Elands Heights, BV = Bastervoetpad, SW = Swaziland.

variation in corolla morphology, especially in the length and shape of the spurs, the shape of the window, and the positioning of the stamens, is the result of adaptation to different species of pollinators. The purpose of this study was to evaluate that hypothesis by measuring floral variation and examining its effect on the pollination of each *Diascia* species in the Drakensberg. In particular, we were interested in whether each species had its own specific pollinator or whether only one or a few species of bees pollinated all of the *Diascia* species. Since Hilliard & Burtt (1984) also noted that several *Diascia* species may occur in close proximity, we were interested in the extent to which pollinators partitioned the *Diascia* species in these areas.

This study of the Drakensberg *Diascia* species is part of a larger project designed to examine the association of oil-collecting bees and oil-producing flowers in southern Africa with the aim of studying the degree to which bees and flowers are mutually dependent and to answer specific questions that remain pertaining to the oil-collecting phenomenon in general.

METHODS

FLORAL MORPHOLOGY

At least one collection of each of the 12 species of *Diascia* occurring in the Drakensberg was cultivated in a 35 cm pot under 30% shade cloth at the Drakensberg Botanic Gardens, Harrismith, during the summers of 1983–1984 and 1984–1985. These plants were used for crossing experiments and for flower measurements.

Four floral characters were measured for each *Diascia* collection: corolla length, anther–window distance, spur length, and gland patch length within each spur. Ten flowers were randomly selected from actively growing portions of each

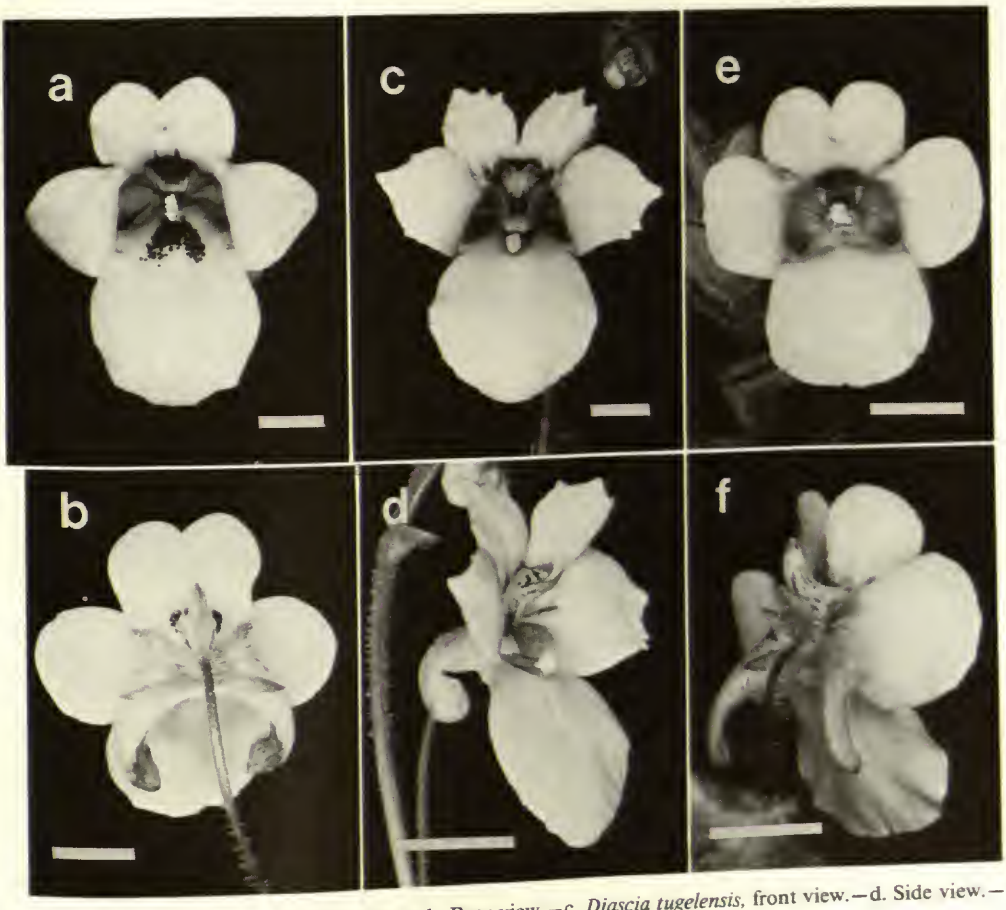

FIGURE 3.—a. *Diascia vigilis,* front view.—b. Rear view.—c. *Diascia tugelensis,* front view.—d. Side view.—e. *Diascia stachyoides,* front view.—f. Rear view. Scale lines = 0.5 cm.

plant. Measurements were made to the nearest 0.5 mm with vernier calipers. Corollas were measured from the top of the upper lobes to the bottom of the lower lobes. To compensate for differences in spur shape among the species, a wire was inserted into the spur to straighten it. The wire was marked at the spur opening and then withdrawn and measured. Spur length was measured from the spur tip to the upper surface of the corolla invagination that partitions the two spur openings anterior to the filaments. Anther–window distance was measured from the upper edge of the window to the anterior side of the anthers. For species with development of two different pairs of stamens (*D. anastrepta, D. megathura,* and *D. purpurea*) the anther–window distance was measured to the lower fertile stamens (Fig. 4c, e and cf. Hilliard & Burtt, 1984). The length of the oil-secreting area within the spur was measured from the tip to the upper limit of oil-secreting trichomes.

Population samples of flowers collected in the field were measured in the same manner for four of the species in order to compare with single collection measurements. Statistical comparisons between means were made using a one-way analysis of variance.

The breeding system of 11 of the 12 *Diascia* species was investigated by making the following experimental pollinations: (a) self-pollination with no emasculation, (b) self-pollination with emasculation, (c) control (i.e., no manipulation), and (d) cross-pollination after emasculation. Treatment (b) was included because cross-pollinations could not be easily made without removing the stamens.

Two or more *Diascia* species often occur sympatrically in the Drakensberg and Witteberg

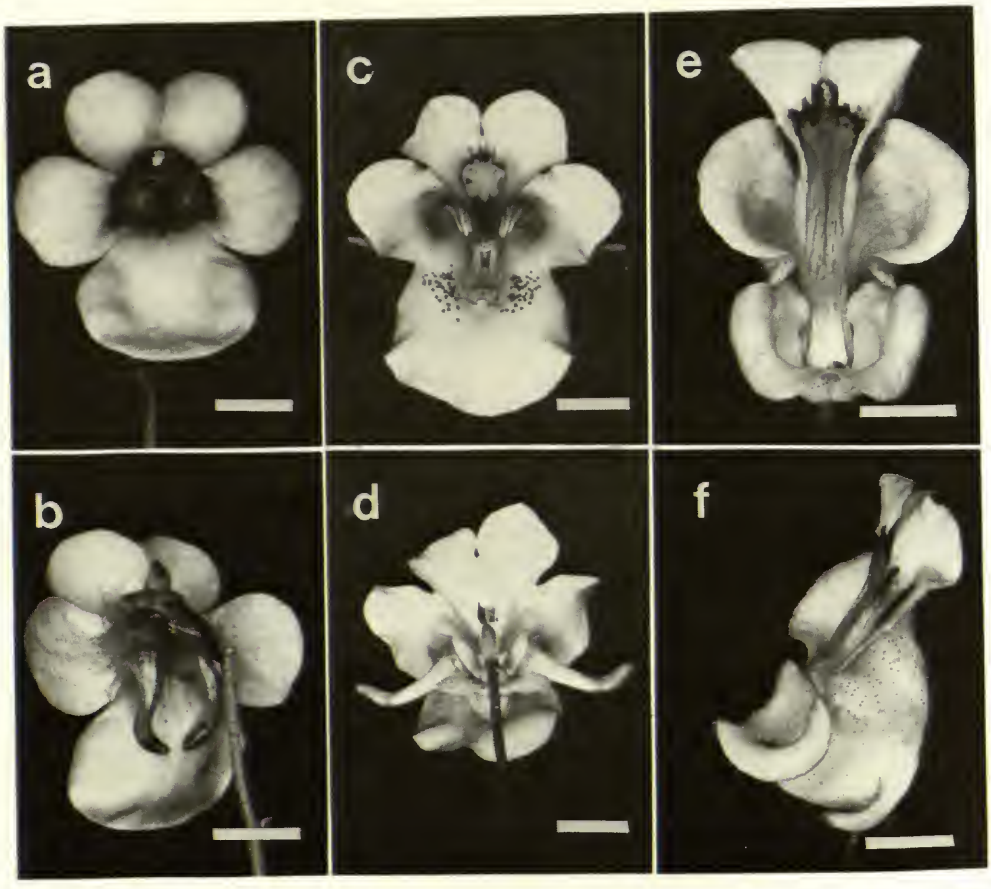

FIGURE 4.—a. *Diascia integerrima,* front view.—b. Rear View.—c. *Diascia anastrepta,* front view.—d. Rear view.—e. *Diascia purpurea,* front view.—f. Side view. Natural orientation of flower is horizontal with front of flower facing down. Scale lines = 0.5 cm.

mountains with substantial overlap in flowering time (Hilliard & Burtt, 1984; Steiner, pers. obs.). Nine such sites were identified, two of which (Royal Natal National Park and Sani Pass) were studied intensively. The elevation and species identity was recorded for each *Diascia* encountered along elevational transects in both areas. At Sani Pass an 11.7 km transect followed the road from 1,740 to 2,760 m, and at Royal Natal collections were made from tributaries of the Tugela at 1,740 m to the top of the Amphitheatre at ca. 2,900 m. Most of the Royal Natal transect was just over the border in Qwaqwa along the road between the entrance to the Witzieshoek Mountain Resort and the parking area at the beginning of the path to the Sentinel and along that path to the plateau above the Amphitheatre.

POLLINATORS

Collections and observations of bees were made in the Drakensberg mountains of Natal, Orange Free State, Qwaqwa, Lesotho, Transkei, and the Cape, as well as the Witteberg mountains in the northeastern Cape (Fig. 2) during January and February of 1984 and 1985. The amount of time spent in observation and collection of bees from the different *Diascia* species varied between sites and was highly dependent on weather conditions.

Foreleg and body lengths of males and females of each *Rediviva* species collected were measured with a dissecting microscope equipped with an occular micrometer. Pollen placement on the bees was noted and then samples were removed and mounted in a mixture of polyvinyl-lactophenol

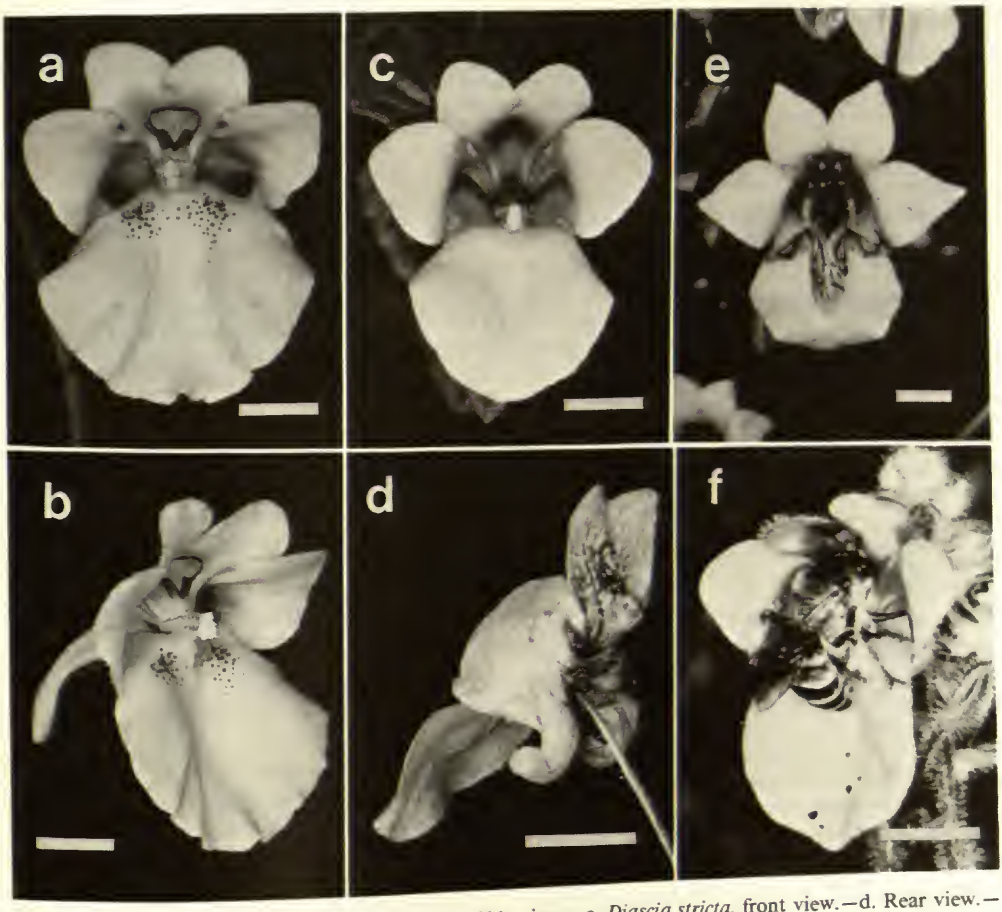

FIGURE 5.—a. *Diascia barberae*, front view.—b. Side view.—c. *Diascia stricta*, front view.—d. Rear view.—e. *Rediviva neliana* visiting *Diascia tugelensis*.—f. *R. neliana* visiting *Diascia fetcaniensis*. Scale lines = 0.5 cm.

and identified through comparisons with voucher material. Vouchers of the bees have been deposited in the South African Museum, while plant vouchers are at NBG.

RESULTS

FLORAL MORPHOLOGY

Figures 3–5 show that *Diascia* species vary in overall size, spur shape and length, and anther–window distance. The species illustrated encompass most of the variation exhibited by the 12 Drakensberg species. For drawings and authorities of all of the species in the Drakensberg except *D.* "*barberae*" see Hilliard & Burtt (1984).

COROLLA SIZE

Corolla lengths varied from 15.28 ± 0.71 to 26.47 ± 1.04 mm (Table 1). In addition to significant differences between species in corolla size, there were significant differences between individuals of the same species from the same population (*D.* "*barberae*" 580A and B, $P < 0.001$) and from different populations (*D. anastrepta* 588 and 592A, $P < 0.001$; *D. cordata* 591 and 582, $P < 0.01$; *D. stachyoides* 82/83 and 534A, $P < 0.05$. However, just the opposite was found for *D. stricta* (548A and B), which did not differ significantly between collections from the same population, and for *D. integerrima* (005/32, 004/236 and 15/82) and *D. fetcaniensis* (535 and 537A), which did not differ significantly between different localities.

SPUR AND WINDOW SHAPE

There are three main spur orientations and various types of tip curvature contributing to the overall spur shape of the 12 *Diascia* species. Spurs

TABLE 1. Mean corolla sizes of *Diascia* collections, N = 10.

Diascia sp.	Collection No.	Corolla Length (mm) ± s.d.	Collection Location
D. cordata	582	15.28 ± 0.71	Sani Pass, Natal
D. stachyoides	534A	16.60 ± 0.75	Barkly Pass, E. Cape
D. stricta	833	15.80 ± 0.34	Joubert's Pass, E. Cape
D. cordata	591	16.59 ± 1.24	Giant's Castle, Natal
D. stachyoides	82/83	16.60 ± 0.75	Qachas Nek, Transkei
D. stricta	548B	16.79 ± 0.83	Ben Macdhui, E. Cape
D. stricta	548A	16.93 ± 1.14	Ben Macdhui, E. Cape
D. integerrima	005/32	17.26 ± 1.41	Otto du Plessi's Pass, E. Cape
D. integerrima	004/236	17.42 + 0.94	Cathedral Peak, Natal
D. barberae	3/82	17.68 ± 1.21	Platberg, OFS
D. anastrepta	588	17.93 ± 1.17	Sani Pass, Natal
D. purpurea	005/152	18.27 ± 0.59	Royal Natal, Natal
D. integerrima	15/82	18.31 ± 1.56	Lundean's Nek, E. Cape
D. fetcaniensis	537A	19.09 ± 1.06	Elands Heights, E. Cape
D. fetcaniensis	535	19.33 ± 1.96	Basterovoetpad, E. Cape
D. vigilis	568	20.36 ± 1.11	Royal Natal, Natal
D. tugelensis	571	20.41 ± 1.02	Royal Natal, Natal
D. megathura	005/109	20.53 ± 1.17	Garden Castle, Natal
D. megathura	578	21.35 ± 0.84	Garden Castle, Natal
D. "barberae"	580C	22.41 ± 0.84	Garden Castle, Natal
D. anastrepta	592A	22.83 ± 1.20	Cathedral Peak, Natal
D. tugelensis	(Witches)*	23.03 ± 1.95	Royal Natal, Natal

* Flowers collected from a single individual in the field.

project straight downward parallel to the floral axis (*Diascia tugelensis*, Fig. 3d; *D. integerrima*, Fig. 4b; *D. purpurea*, Fig. 4f; *D. stricta*, Fig. 5d), diverge outward at right angles to the axis (*D. anastrepta*, Fig. 4d, and *D. megathura*) or diverge out at ca. 45° and then curve downward (*D. vigilis*, Fig. 3b; *D. stachyoides*, Fig. 3f; *D. barberae*, Fig. 5b; and *D. "barberae"*). The tips of the spurs, usually the last few millimeters, are either straight (*D. megathura* and *D. cordata*), forward curving (*D. stricta*, *D. fetcaniensis*, *D. barberae*, and *D. "barberae"*), upward curving (*D. anastrepta*), inward curving (*D. integerrima*, *D. purpurea*, and *D. vigilis*), or swollen and inward curving (*D. tugelensis*). Differences can also be seen in the window shapes of the various species, ranging from a drawn-out cone in *D. stachyoides* to a moderately concave window in *D. vigilis* to a flat or only shallowly concave area in *D. megathura*, *D. anastrepta*, and *D. purpurea* (cf. Hilliard & Burtt, 1984). The window of *D. integerrima* is moderately concave but completely obscured by inclusion of the stamens.

SPUR AND GLAND PATCH LENGTHS

Spur lengths of the Drakensberg *Diascia* species varied from 5.51 ± 0.34 to 11.46 ± 0.48 mm (Table 2). Only for two species were two collections from the same population measured and in one case (*D. "barberae"* 580A versus 580C) spur lengths were significantly different ($P < 0.001$), but in the other case (*D. stricta* 548A versus 548B) there was no significant difference ($P > 0.10$). Similarly, there were cases in which plants of the same species from different locations had significantly different ($P < 0.001$) spur lengths, such as *D. stachyoides*, *D. anastrepta*, and *D. cordata*, and cases where there were no significant differences between different collection localities (*D. stricta* and *D. fetcaniensis*). There was also no correlation between corolla size and spur length, nor was there a correlation between collection location and spur length, as short-spurred species (<7 mm) were found both in the northeastern Cape (Witteberg and Drakensberg), (*D. stricta* and *D. fetcaniensis*) and Natal Drakensberg (*D. "barberae"* and *D. anastrepta* 588). Although most of the long-spurred species (≥10 mm) occur in the Natal Drakensberg, the longest-spurred collection was *D. barberae* (849) from southern Lesotho.

Average spur lengths for field-collected population samples of *D. purpurea*, *D. tugelensis*, *D. vigilis*, and *D. barberae* were greater than the

TABLE 2. Spur lengths of *Diascia* collections, N = 10.

Diascia sp.	Collection No.	Spur Length (mm) ± s.d.	Gland Patch Length (mm) ± s.d.
D. stricta	833	5.51 ± 0.34	1.80 ± 0.18
D. stricta	548A	5.58 ± 0.28	2.00 ± 0.25
D. stricta	548B	5.80 ± 0.34	2.12 ± 0.21
D. "barberae"	580C	5.87 ± 0.38	2.97 ± 0.29
D. fetcaniensis	537B	6.67 ± 0.67	2.60 ± 0.35
D. anastrepta	588	6.90 ± 0.48	2.76 ± 0.35
D. fetcaniensis	535	6.93 ± 0.49	3.08 ± 0.59
D. stachyoides	543A	7.04 ± 0.42	2.28 ± 0.34
D. integerrima	004/236	7.26 ± 0.20	2.83 ± 0.29
D. "barberae"	580A	7.41 ± 0.33	3.99 ± 0.47
D. tugelensis	571	7.52 ± 0.36	3.64 ± 0.30
D. integerrima	005/32	7.95 ± 0.46	2.94 ± 0.55
D. integerrima	15/82	8.25 ± 0.20	2.34 ± 0.18
D. megathura	005/109	8.63 ± 0.48	3.95 ± 0.18
D. barberae	3/82	8.68 ± 0.28	3.65 ± 0.31
D. vigilis	568	8.70 ± 0.24	3.87 ± 0.23
D. stachyoides	82/83	8.77 ± 0.40	2.28 ± 0.39
D. tugelensis	(Witches)*	8.92 ± 0.34	4.13 ± 0.30
D. anastrepta	592A	9.09 ± 0.34	3.02 ± 0.59
D. cordata	582	9.38 ± 0.36	3.49 ± 0.26
D. megathura	578	10.38 ± 0.52	3.95 ± 0.18
D. cordata	591	10.50 ± 0.40	3.68 ± 0.29
D. purpurea	005/152	11.24 ± 0.72	3.41 ± 0.51
D. barberae	849	11.46 ± 0.48	—

* Flowers collected from a single individual in the field.

corresponding single collection averages measured from cultivated material (Tables 2, 3). However, only *D. barberae* 3/82 came from the same location as the population sample. Even so, except for *D. tugelensis* 571, the single cultivated collections fell within the range of variation exhibited by the population samples.

The oil-secreting trichomes within the spurs of *Diascia* species are not concentrated entirely at the tip but rather extend back from the tip along the inner spur wall (cf. Vogel, 1974: 35, 37; Hilliard & Burtt, 1984). The length of this oil-secreting area or gland patch ranged from 1.80 ± 0.18 to 4.13 ± 0.30 mm (Table 2).

ANTHER–WINDOW DISTANCE

The distance between the upper edge of the window and the anterior edge of the anthers is quite variable due to the different stamen positions within the flowers of the various *Diascia* species (Figs. 3a, c–e; 4a, c, e; 5a–c; Table 4). These range from *D. integerrima* (Fig. 4a), which has erect stamens partially included in the window, to species with paired stamens projecting outward (Figs. 3a, c–e; 5a–c), to species with one, usually sterile, stamen pair projecting outward and one fertile pair projecting downward along the lower corolla lip (Fig. 3c, e). These different positions result in anther–window distances ranging from 0 to 12.91 mm (Table 4).

BREEDING SYSTEM

Results from experimental pollinations of the various *Diascia* species show that they are all self-incompatible and therefore dependent on pollinators to set seed (Table 5).

POLLINATORS

Despite the variation in floral morphology, visitation behavior of *Rediviva* pollinators on the various *Diascia* species was remarkably similar. As a bee alights on the flower, it inserts its forelegs into the two spurs and its mandibles into or on the window. Its middle legs are usually placed at the spur entrances and the hind legs are often hooked on the edge of the lower corolla lip (Fig. 5e, f). Once inside the spurs, the forelegs rub the inner walls in a process that may last from 1–20

TABLE 3. Average spur lengths of field-collected *Diascia* flowers. No more than three flowers were collected from a single plant.

Diascia sp.	Location	No. of Flowers	Spur Length ± s.d. (range)
D. purpurea	Royal Natal Park	30	12.19 ± 0.85 (10.7–13.6)
D. tugelensis	Royal Natal Park, Sentinel	40	9.28 ± 0.59 (8.3–11.0)
D. vigilis	Royal Natal Park, Sentinel	40	9.20 ± 1.11 (7.1–10.9)
D. barberae	Platberg, OFS	39	8.95 ± 0.67 (7.8–10.2)

seconds, but averaging about 4 seconds. The tarsal segments of these oil-collecting bees have finely divided hairs which readily absorb the oil in the spurs. The forelegs are withdrawn from the spurs as the bee takes off from the flower, and the oil is then transferred, using the middle legs, to the scopae on the hind legs where it is stored alone or mixed with pollen until the bee returns to its nest.

Four *Rediviva* species were collected from the twelve Drakensberg *Diascia* species (Fig. 6). Size differences among the bees, although small, are significant. Females of three of the four speices have longer forelegs, relative to body size, than males ($P < 0.001$) (Fig. 6c, d; Table 7). For *R. rufocincta* (Cockerell), as for all the *Rediviva* spp., females are larger (forelegs and body size) than males, but it is the only species in which the ratio of foreleg length/body length is the same for females as for males. The forelegs of females of *R. neliana* are significantly shorter than the forelegs of *Rediviva* sp. nov. 1 females ($P < 0.001$), but body lengths of these two species are not significantly different ($0.05 < P < 0.10$). Both *R. neliana* and *R.* sp. nov. 1 females have significantly shorter forelegs and body lengths than females of *R.* sp. nov. 2 ($P < 0.001$). The length of the tarsal segments, the oil-absorptive portion of the foreleg, also varies among the *Rediviva* species. This is shortest for *R. neliana* and longest for *R.* sp. nov. 1 (Table 7).

Our collection data suggest that *Rediviva neliana* occurs only along the Drakensberg escarpment, which forms Lesotho's eastern border with Natal and south to the mountains of the northeastern Cape but not in the Witteberg (Fig. 7). The Witteberg and the highlands of Lesotho are occupied by *R.* sp. nov. 1. The two species overlap at Sani Pass and perhaps at other locations along the escarpment, but although *R.* sp. nov. 1 occurs near Oxbow, Lesotho, it has not been collected at the Sentinel, which is only about 20 km away. *Rediviva neliana* has been collected near Joubert's Pass at Lady Grey (cf. Fig. 2) (Michener, 1981), but this is a distinct subspecies (Whitehead, in prep.). *Rediviva rufocincta* has been recently collected at Sani Pass on *Bowkeria* (Manning & Brothers, 1986).

Elevation does not appear to play a role in the separation of *Rediviva neliana* and *R.* sp. nov. 1 except perhaps at the lower limit, since their elevational ranges are similar (1,740–2,780 m and 2,140–2,710 m respectively). *Rediviva* sp. nov. 2 (1,740–2,360 m) overlaps with *R. neliana* at Sani Pass and Royal Natal Park, while *R. rufocincta* overlaps with both *R. neliana* at Royal Natal National Park and with *R.* sp. nov. 1 at Joubert's Pass.

TABLE 4. Mean anther–window distances of *Diascia* collections, N = 10.

Diascia sp.	Collection No.	Anther–Window Distance (mm) ± s.d.
D. integerrima	004/236	0.0
D. integerrima	005/32	0.0
D. integerrima	15/82	0.0
D. stachyoides	534A	2.02 ± 0.27
D. stachyoides	82/83	2.74 ± 0.31
D. barberae	3.82	3.06 ± 0.20
D. cordata	591	3.18 ± 0.26
D. vigilis	568	3.22 ± 0.34
D. fetcaniensis	535	3.63 ± 0.59
D. cordata	582	3.78 ± 0.25
D. stricta	548B	4.77 ± 0.33
D. fetcaniensis	537A	4.80 ± 0.45
D. stricta	548A	5.24 ± 0.30
D. stricta	833	5.24 ± 0.52
D. tugelensis	571	5.34 ± 0.52
D. tugelensis	(Witches)*	5.63 ± 0.62
D. "barberae"	580C	6.13 ± 0.47
D. anastrepta	592A	6.38 ± 0.42
D. anastrepta	588	7.64 ± 0.55
D. "barberae"	580A	7.72 ± 0.35
D. megathura	005/109	9.92 ± 0.53
D. megathura	578	11.34 ± 0.42
D. purpurea	005/152	12.91 ± 0.56

* Flowers collected from a single individual in the field.

TABLE 5. Results of *Diascia* crossing experiments.

Diascia sp.	Collection No.	Control frs/fls[a]	Self + E[b] frs/fls	Self, no E frs/fls	% fr Set of Total Selfs	N	% fr Set of Crosses	N	Crosses vs. Selfs[c] χ^2 value	*P*-value
D. anastrepta	68/82	0/15	0/20	0/15	0.0	35	—	—	—	—
D. anastrepta	587	0/15	1/15	0/15	3.3	30	60.0	15	18.58	$P < 0.005$
D. barberae	3/82	0/14	0/15	0/15	0.0	30	100.0	15	45.00	< 0.005
D. "barberae"	580A	0/15	1/14	0/20	2.9	34	60.0	15	20.86	< 0.005
D. cordata	3/83	0/16	0/15	0/20	0.0	45	72.2	18	40.96	< 0.005
D. fetcaniensis	78/83	0/10	0/11	0/13	0.0	24	93.3	15	34.94	< 0.005
D. fetcaniensis	14/82	—	—	—	0.0	6	93.3	15	—	—
D. fetcaniensis	13/82	0/6	0/14	1/14	3.6	28	93.3	15	34.65	< 0.005
D. integerrima	41/82	0/14	0/14	1/15	3.4	29	90.0	20	37.35	< 0.005
D. integerrima	004/236	0/15	0/15	1/15	3.3	30	92.3	13	4.04	< 0.005
D. purpurea	89/83	0/15	0/15	—	0.0	15	60.0	15	12.86	< 0.005
D. stachyoides	82/83	0/14	0/14	0/15	0.0	29	80.0[d]	10	29.19	< 0.005
D. stricta	548C	0/15	0/15	0/15	0.0	30	93.3	15	40.65	< 0.005
D. stricta	833	—	—	0/10	0.0	10	90.0	10	16.36	< 0.005
D. tugelensis	10/82	0/13	0/15	0/15	0.0	30	86.7	15	36.56	< 0.005
D. tugelensis	571	0/14	—	0/20	0.0	20	94.2	17	33.17	< 0.005
D. vigilis	95/76	0/17	0/20	1/21	2.4	41	54.8	31	25.85	< 0.005
D. vigilis	11/82	0/15	0/16	2/13	6.9	29	33.3	15	5.16	< 0.025
D. vigilis	595	—	—	0/20	0.0	20	65.0	20	19.26	< 0.005
D. vigilis	568	—	—	0/20	0.0	20	50.0	20	13.33	< 0.005
					$\bar{x} = 1.36$ ±2.01		$\bar{x} = 76.9$ ±19.33			

[a] Fruits set per flowers crossed.
[b] E = emasculation.
[c] Two-way contingency test.
[d] Interspecific cross (× *D. fetcaniensis*).

It is obvious (Table 6) that five of the 12 *Diascia* species are pollinated by more than one bee species even in the same location and that similarly *R. neliana, R.* sp. nov. 1, and *R.* sp. nov. 2 all visit more than one *Diascia* species. *Rediviva neliana* was collected from nine *Diascia* species, *Rediviva* sp. nov. 1 from six, and *R.* sp. nov. 2 from two.

Rediviva species were not the only bee visitors. Small, typically ca. 6 mm long, bees (Halictidae and Megachilidae) were occasionally encountered on 8 of the 12 species, but they were not always present. They tended to be most abundant when *Diascia* flowers were present in large numbers and in such situations may effect some pollination. However, we would expect them to be less effective in situations where plants are more widely spaced, a common condition in *Diascia,* as the pollen-collecting bees tend to spend more time per flower and move less frequently and shorter distances between flowers than *Rediviva* species (pers. obs.). These bees ignore the translucent window and oil-producing spurs and concentrate solely on removing pollen from the anthers (Manning in Hilliard & Burtt, 1984; pers. obs.).

PATTERNS OF CO-OCCURRENCE

We found two or more *Diascia* species growing sympatrically at nine localities, while Hilliard & Burtt (1984) report two additional areas of sympatry (cf. Table 8). Based on our observations and data from Hilliard & Burtt (1984), it is likely that co-occurrence of two or more *Diascia* species is common in the Drakensberg.

Little information is available on the flowering patterns of these species except for collection dates cited by Hilliard & Burtt (1984) and our own observations. Most Drakensberg *Diascia* species flower for two to four months with a peak in January or February. Although differences occur between flowering peaks, these do not preclude overlap of several weeks to two months at a given

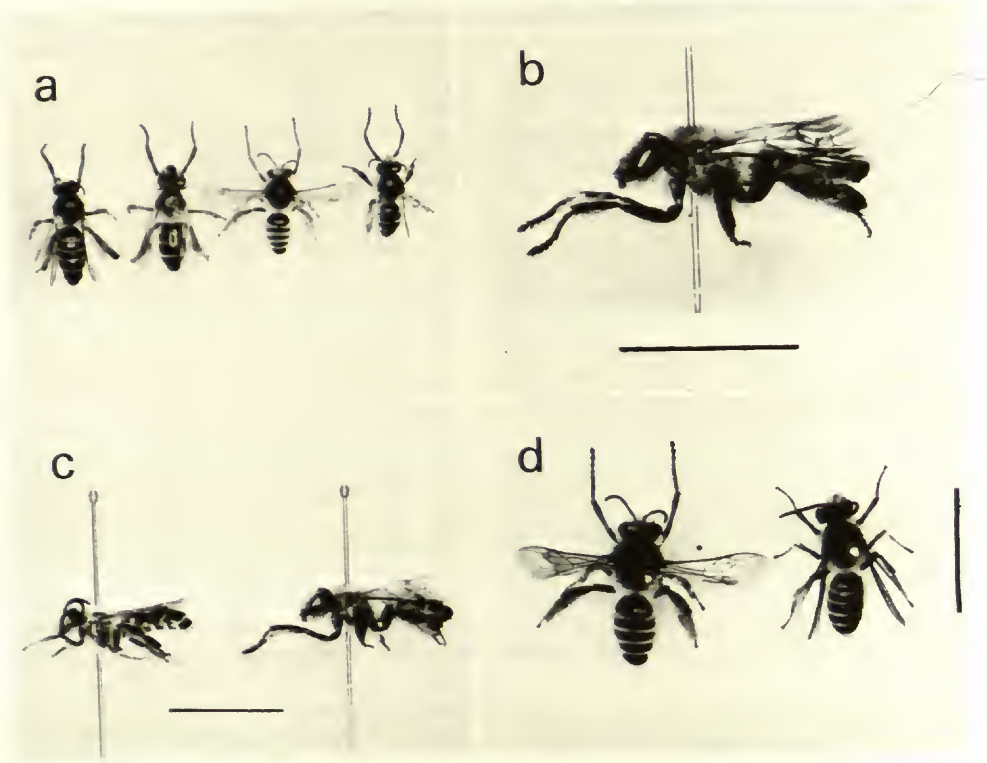

FIGURE 6.—a. From left to right: females of *Rediviva rufocincta*, *R.* sp. nov. 2, *R.* sp. nov. 1, and *R. neliana*.—b. *Rediviva* sp. nov. 2 female.—c. *Rediviva* sp. nov. 2 male (left) and female (right).—d. *Rediviva*. sp. nov. 1 female (left) and male (right). Scale bars = 1.0 cm.

location. At all of the sympatry locations flowering times overlapped. More detailed studies are required to determine the extent of this overlap.

Although female bees were caught at each of the sites, except Sehlabathebe (Table 8), they were not always caught on each *Diascia* species at a given site. Analysis of pollen on the bees, however, often indicated visits to other *Diascia* species that we may have overlooked in the area. For example, we did not see *D. integerrima* at Qachas Nek (Table 8), but its occurrence was inferred from the position of *Diascia* pollen found on bees captured on *Wahlenbergia undulata*. An herbarium collection of *D. integerrima* from this area supports this inference (*Brooke 38*, BM).

The largest concentration of *Diascia* species in the Drakensberg was found at Sani Pass, where five species occur (Fig. 8). Three different species of *Rediviva* were captured on four of the *Diascia* species (Fig. 8, Table 6). *Rediviva* sp. nov. 2 was collected on *D. cordata*; *R.* sp. nov. 1 was collected from *D. integerrima*, *D. cordata*, and *D. anastrepta*; while *R. neliana* was collected from *D. integerrima*, *D. cordata*, and *D. megathura*. No observations were made on *D. barberae* but, based on the distribution patterns of the bees (Fig. 7), it is likely to be pollinated by *R.* sp. nov. 1. The indiscriminate use of the available *Diascia* species is further indicated by an analysis of pollen found on collected bees, which shows that an individual bee may visit up to three different *Diascia* species (Table 9).

The three overlapping *Diascia* species (*D. megathura*, *D. integerrima*, and *D. cordata*) all place pollen on different parts of the bee's body (Fig. 9). Even though *D. barberae* places pollen in a similar position to *D. cordata*, and *D. anastrepta* and *D. megathura* have similar deposition patterns, these species pairs do not overlap along the transect. One-third (N = 18) of *R.* sp. nov. 1 and three of four *R. neliana* bees collected in the region of maximum flower and bee overlap along the elevational transect carried two or more species of *Diascia* pollen (Table 9).

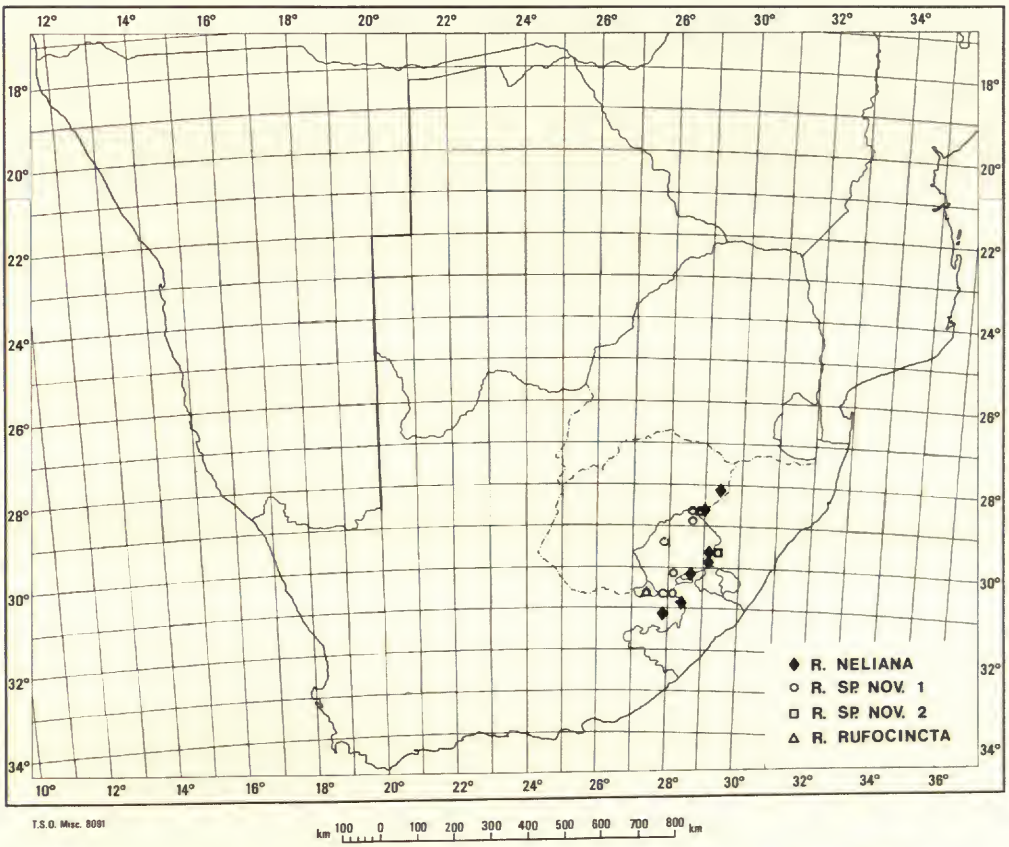

FIGURE 7. Distribution of *Rediviva* bees in the Drakensberg of southern Africa based on our collections only, but see text.

In the Royal Natal National Park area, two *Rediviva* species were collected from the three *Diascia* species (Fig. 10). A third species, *R. rufocincta,* is known from this area but it has not been collected on *Diascia* here, although it has elsewhere (Table 6). *Rediviva* sp. nov. 2 was the main visitor to *D. purpurea* (15 of 17 bees), while two *R. neliana* individuals were also collected from *D. purpurea.* The occurrence of all three *Diascia* species in close proximity is probably rare in the Royal Natal area, but *D. vigilis* and *D. purpurea* as well as *D. vigilis* and *D. tugelensis* can easily be found within 20 meters of each other.

None of the bees that were collected on *Diascia purpurea* carried pollen of other *Diascia* species, but most of the bees were collected below the region of overlap of *D. purpurea* and *D. vigilis.* At a higher elevation (2,340 m), 9.3% (N = 75) of the *R. neliana* bees caught on *D. vigilis* carried *D. purpurea* pollen. At a site near the Sentinel where *D. vigilis* and *D. tugelensis* grow intermingled, 81.8% (N = 22) of the bees captured carried pollen of both species (Table 9). *Diascia vigilis* and *D. tugelensis* deposited pollen on the underside of the bee (Fig. 9), but because of a significant difference ($P < 0.001$) in mean anther to window distance of the two species (3.12 ± 0.35 mm, N = 40 vs. 6.12 ± 0.68 mm, N = 40, respectively), pollen overlap on the bees was minimal.

DISCUSSION

SPECIES SPECIFICITY

There is little evidence to support the hypothesis that floral variation exhibited by the Drakensberg *Diascia* species is the result of selection by different pollinator species. Our data indicate that pollination in at least 10 of the 12 species

TABLE 6. Bees caught on (females) or patrolling (males) *Diascia* flowers.

Diascia sp.	*Rediviva* sp.	Females (N)	Males (N)	Location
D. anastrepta	*R.* sp. nov. 1	3		Sani Pass, Natal
	R. sp. nov. 1	10	5	Blue Mountain Pass, Lesotho
	R. sp. nov. 1	2		Moteng Pass, Lesotho
D. barberae	*R.* sp. nov. 1	5	1	Lebelonyane Pass, Lesotho
	R. neliana	5		Platberg, OFS
D. "barberae"	*R.* sp. nov. 1	3		Oxbow, Lesotho
D. cordata	*R. neliana*	17		Sani Pass, Natal
	R sp. nov. 2	3		Sani Pass, Natal
D. fetcaniensis	*R. neliana*	10		Bastervoetpad, E. Cape
	R. neliana	15		Elands Heights, E. Cape
	R. sp. nov. 1	1	2	Naudesnek, E. Cape
D. integerrima	*R. neliana*	8	2	Sani Pass, Natal
	R. sp. nov. 1	16		Sani Pass, Natal
	R. sp. nov. 1	4		Naudesnek, E. Cape
	R. sp. nov. 1	5	1	Carlisleshoek, E. Cape
	R. sp. nov. 1	3		Joubert's Pass, E. Cape
	R. sp. nov. 1	1	2	Blue Mountain Pass, Lesotho
D. megathura	*R. neliana*	1	1	Garden Castle, Natal
	R. neliana	1		Sani Pass, Natal
D. purpurea	*R.* sp. nov. 2	17	2	Royal Natal Park, Natal
	R. neliana	2		Royal Natal Park, Natal
D. stachyoides	*R. neliana*	1		Qachas Nek, Transkei
D. stricta	*R.* sp. nov. 1	1		Ben Macdhui, E. Cape
	R. sp. nov. 1	6	1	Naudesnek, E. Cape
D. tugelensis	*R. neliana*	17		Sentinel, Qwaqwa/Royal Natal
D. vigilis	*R. neliana*	78		Pudding, Qwaqwa/Royal Natal
	R. neliana	7		Sentinel, Qwaqwa/Royal Natal

(>83%) can be linked to one of two *Rediviva* species. In some cases a single *Diascia* species may be pollinated by two different *Rediviva* species even in the same location, and in other cases a single *Rediviva* species may pollinate more than one *Diascia* in the same location. Despite the lack of specificity between *Rediviva* and *Diascia* species, the fact that all Drakensberg *Diascia* species are self-incompatible means that they are totally dependent on bees (primarily oil-collecting bees) for sexual reproduction.

The morphological differences between *Rediviva neliana* and *R.* sp. nov. 1 cannot account for specific differences in floral morphology of the species they pollinate. *Rediviva neliana* pollinates species with short spurs (i.e., *D. fetcaniensis*) to long spurs (*D. cordata*), from small flowers (*D. cordata*) to large flowers (*D. tugelensis*), from flowers with anthers in the window (*D. integerrima*) to anthers well away from the window (*D. megathura* and *D. purpurea*), and from flowers with a flat window (*D. megathura*) to flowers with cone-shaped windows (*D. stachyoides*). The pattern is similar for *Rediviva* sp. nov. 1 (Table 6). Only *R.* sp. nov. 2 appears to be limited in the number of *Diascia* species it visits. It has been collected primarily from *D. purpurea* but has also been found on *D. cordata*.

TABLE 7. Size comparisons of *Rediviva* species from the Drakensberg, means ± s.d. (range).

Rediviva sp.	Foreleg Length of Females	Length of Female Tarsal Segments	Foreleg Length/Body Size of Females
R. neliana	10.93 ± 0.74 (9.20–11.60)	1.74 ± 0.17 (1.41–2.01)	1.03 ± 0.06 (0.93–1.12)
R. sp. nov. 1	12.02 ± 0.39 (11.60–13.00)	2.38 ± 0.14 (2.08–2.67)	1.08 ± 0.04 (1.01–1.14)
R. sp. nov. 2	12.82 ± 0.58 (11.67–13.25)	1.99 ± 0.06 (1.92–2.09)	1.03 ± 0.06 (0.90–1.07)
R. rufocincta	10.71	1.88	0.75

diviva sp. nov. 2 has the longest forelegs of the Drakensberg species and, unlike *R. neliana* and *R.* sp. nov. 1, has been collected only on long spurred *Diascia* species.

The lack of adequate collections of *Rediviva rufocincta* makes prediction of its host specificity difficult, but due to its lack of female leg elongation (Table 7), rarity on *Diascia* species and observation on *Bowkeria* (Manning & Brothers, 1986), it is probably associated primarily with *Bowkeria* or other, as yet unknown, oil-secreting flowers. One other *Rediviva, R. colorata* Michener, is also known from eastern southern Africa. It has been collected only in the Karkloof area of the Natal Midlands and has yet to be collected from any oil-secreting flowers (Manning & Brothers, 1986). *Diascia cordata* is known from Karkloof (Hilliard & Burtt, 1984), and although apparently uncommon there, it may be visited by *R. colorata.*

Most of the observations made by Manning & Brothers (1986) agree with ours despite their lack of quantitative data. However, because of the superficial nature of their study, they have been too quick to attribute specificity where it does not exist. They suggest that *Rediviva* sp. (our *Rediviva* sp. nov. 2) is specific to *Diascia purpurea* based on the collection of a single bee. Our data show that *Rediviva* sp. nov. 2 is not specific to *Rediviva purpurea* but visits *D. cordata* as well. And similarly, *D. purpurea* is not visited solely by *R.* sp. nov. 2 but also by *R. neliana* (= *R. politissima*). They also report that the legs of *Rediviva* sp. are not as elongated as *R. politissima* but fail to provide any measurements to confirm this. Data in Table 7, however, show that this species has forelegs that are elongated to the same extent, relative to body size, as *R. politissima* (= *neliana*) and in absolute terms they are longer. Manning & Brothers (1986) also suggest that *R. rufocincta* is specific to *Bowkeria,* but our collections from *Diascia integerrima* indicate that it may occasionally utilize other oil plants as well. At Sani Pass, they did not realize that there were two species of *Rediviva* commonly on *Diascia, R.* sp. nov. 1 and *R. neliana.*

TABLE 7. Continued.

N	Foreleg Length/Body Size of Males	N
12	0.77 ± 0.04 (0.72–0.86)	13
12	0.82 ± 0.05 (0.75–0.90)	13
6	0.72 ± 0.04 (0.65–0.77)	5
2	0.76	1

SPUR AND LEG LENGTHS

There are two important characters that influence the oil-collecting relationship in *Diascia*: the overall spur length and the extent of the oil-secreting region within the spur. Similarly, it is the overall leg length and the length of the oil absorptive region on the leg which are important for the bees. Only one of the four *Rediviva* species was collected from a *Diascia* species with an average spur length longer than its average foreleg length. This was *R. neliana* on *D. purpurea.* However, the ranges in spur and leg length overlap (Tables 2, 7). Still, this may explain why the larger *R.* sp. nov. 2 appears to be the primary pollinator of *D. purpurea.*

An additional factor that complicates the relationship between leg and spur length is the fact that the tip of the foreleg does not have to reach the tip of the spur in order to absorb at least some oil. For example, if the spur length is 12.19 mm (*D. purpurea*) and the gland patch length is 3.41 mm (*D. purpurea*), a bee with a leg length of 10.93 mm (*R. neliana*) can overlap the gland patch by 2.15 mm, which is 0.41 mm longer than the absorptive portion of its tarsus. However, although the distribution of trichomes in the gland patch was not quantified, the greatest concentration, and hence the most oil, is invariably in the portion nearest the spur tip.

The position of the bee on the flower is such that a small portion of the top of the foreleg is often just back from the spur opening. This causes the effective leg length (that portion actually in the spur) to be slightly less than the measured length. This portion, although difficult to estimate, appeared from photographs to be ≤1 mm. If this portion were estimated to be 1.0 mm, the legs of *Rediviva* species would still be able to reach the spur tips of most of the *Diascia* species, with the exception of *R. neliana* on *D. megathura* 578, *D. cordata* 591, and *D purpurea* 005/152 and *R.* sp. nov. 1. on *D. barberae* 849.

Behavioral adjustments of the bees on the flower can also influence the effective leg length. *Rediviva neliana* was commonly observed to extend its reach by 1–2 mm when leaning to the right or left of center on *D. vigilis* flowers.

COMPETITION AND POLLINATION

There are two potential types of competition among sympatric plant species with respect to

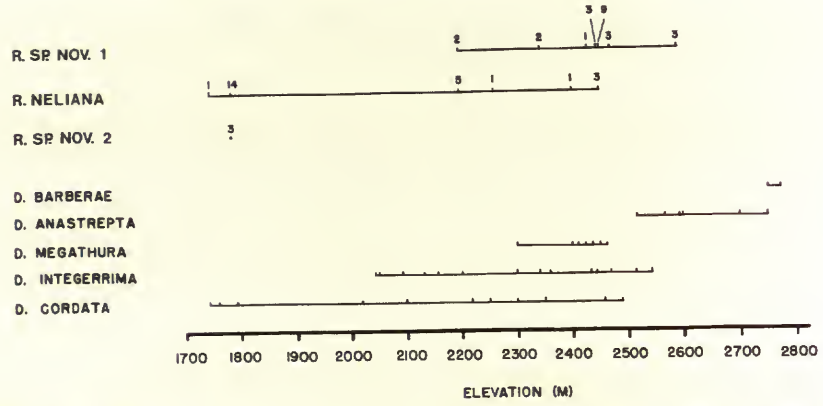

FIGURE 8. Distribution of *Rediviva* and *Diascia* species along an elevational transect at Sani Pass. Total length of transect ca. 11.7 km. Numbers indicate the number of bees collected at the indicated elevation, while marks on the *Diascia* lines are collections or sightings.

pollination (Waser, 1983; Rathcke, 1983). The first of these has been termed competition for pollinator visitation by Rathcke and competition through pollinator preference by Waser; it results when each competing species suffers reduced pollinator visitation and lowered reproductive success.

The second type of competition is due to improper (Rathcke, 1983) or interspecific (Waser, 1983) pollen transfer. Improper pollen transfer can result in a decrease in male function through pollen loss or a decrease in female function as a result of physical (stigma clogging) or chemical interference with proper (conspecific) pollen (Armbruster & Herzig, 1984; Stucky, 1985) or through the production of inviable seed, sublethal or sterile hybrids, or even fully fertile hybrids, if postzygotic selection excludes them from the habitat (cf. Kyhos et al., 1981).

Our data and observations by Hilliard & Burtt (1984) show that *Diascia* species and sometimes *Rediviva* species occur in close proximity. Under such conditions one might expect either type of reproductive competition among the plants and perhaps competition between the bees for oil. Too little is known about the overall resource requirements of the bees to determine whether they compete in areas of overlap, and therefore

TABLE 8. Sites where *Diascia* spp. co-occur. INT = *integerrima*, STR = *stricta*, FET = *fetcaniensis*, STA = *stachyoides*, MEG = *megathura*, ANA = *anastrepta*, BAR = *barberae*, "BAR" = "*barberae*," COR = *cordata*, PUR = *purpurea*, TUG = *tugelensis*, VIG = *vigilis*.

Location	*Diascia* sp.						
	INT	STR	FET	STA	MEG	ANA	BAR
Blue Mountain, Lesotho	+					+	
Joubert's Pass, E. Cape	+	+					
Carlisleshoek, E. Cape	+	+					
Ben Macdhui, E. Cape*	+	+	+				
Naudesnek, E. Cape	+	+					
Qachas Nek, Transkei	+			+			
Sehlabathebe, Lesotho	+				+		
Garden Castle, Natal	+				+		
Sani Pass, Natal	+				+	+	+
Loteni, Natal*						+	
Royal Natal Park, Natal							

* Data from Hilliard & Burtt (1984).

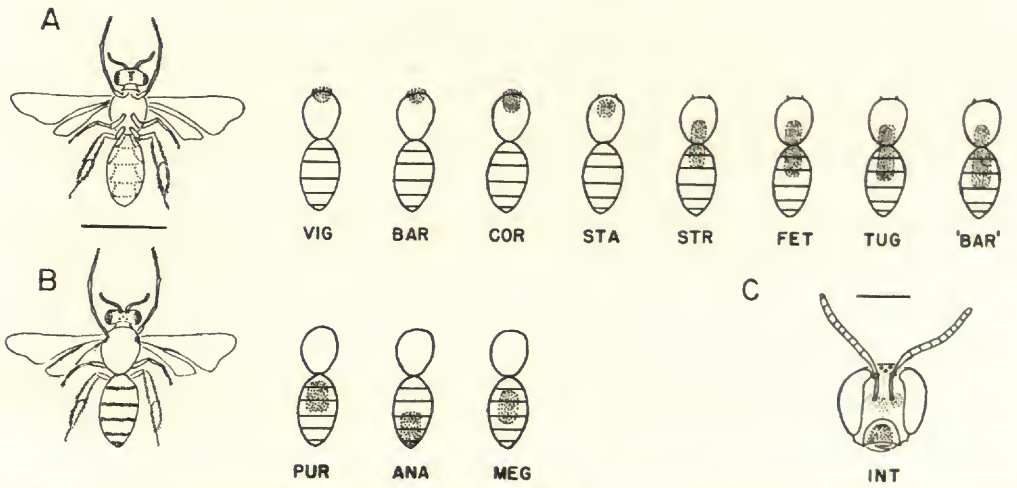

FIGURE 9. Pollen deposition patterns on *Rediviva* species collected from the indicated *Diascia* species. VIG = *vigilis*, BAR = *barberae*, COR = *cordata*, STA = *stachyoides*, STR = *stricta*, FET = *fetcaniensis*, TUG = *tugelensis*, 'BAR' = "*barberae*," PUR = *purpurea*, ANA = *anastrepta*, MEG = *megathura*, INT = *integerrima*.—A. Ventral surface of *Rediviva*.—B. Dorsal surface.—C. Head. Scale lines = 10 mm for A, B; 2.5 mm for C.

little further can be said. There is greater evidence to suggest possible competition between *Diascia* species for pollination.

There are several possible ultimate outcomes of competition for pollination which lead to stable coexistence (Waser, 1983). These include divergence in floral color, floral morphology, and/or flowering time. There are no marked color differences, either UV or visible (Steiner, unpubl.), among the *Diascia* species, and overlap in flowering time is substantial. Therefore, we would expect coexistence to be predicated on differences in floral morphology or pollinator behavior (i.e., floral constancy). Clearly there are differences in flower size as well as spur length and shape, but it is the anther–window distance that is most important, as it determines pollen placement on the visiting bee. Differences in anther position among the *Diascia* species is probably the result of competition due to improper/interspecific pollen transfer. Similar shifts in pollen placement have been reported for sympatric bumblebee pollinated species of *Pedicularis* (Scrophulariaceae) in California, but in this case pollen separation was incomplete and the main factor allowing coexistence was believed to be ethological isolation (i.e., individual constancy of the pollinators) (Sprague, 1962). We have no data on the frequency of interspecific movements of *Rediviva* between *Diascia* species, but examination of pollen carried by bees in zones of sympatry (Table 9) suggests that floral constancy is weak, at best, among *Rediviva* pollinators. Differences in pollen placement have also been reported for sympatric bee-pollinated *Polygala* species (Brantjes, 1982) and for coexisting butterfly (Levin & Berube, 1972), bat (Howell, 1977), and hummingbird (Stiles, 1975; Carpenter, 1978; Waser, 1978; Brown & Kodric-Brown, 1979) pollinated plants.

Even though differences in pollen placement may be attributed to interspecific competition for pollen transfer, we cannot suggest that the patterns described are due to competition between

TABLE 8. Continued.

Diascia sp.				
"BAR"	COR	PUR	TUG	VIG
+				
+				
	+			
		+		
		+	+	+

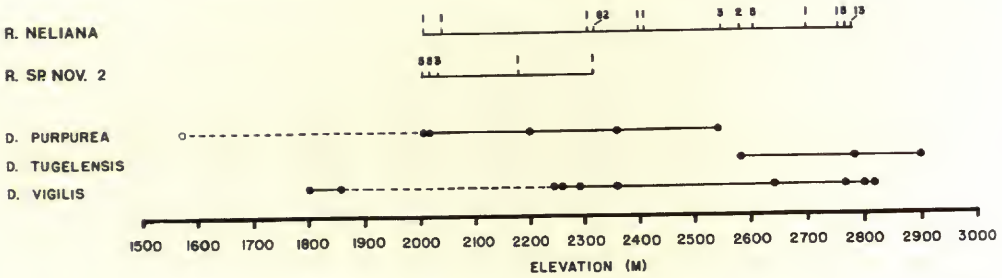

FIGURE 10. Distribution of *Rediviva* and *Diascia* species along an elevational transect through Royal Natal National Park and Qwaqwa to the Amphitheatre. Numbers indicate the number of bees collected at the indicated elevation, while solid circles on the *Diascia* lines are collections. Open circle is from Hilliard & Burtt (1984). Broken lines indicate that presence is doubtful due to very steep relief.

the presently co-occurring species without a better knowledge of their evolutionary histories. For example, the divergence in anther position of *Diascia integerrima* could have evolved through competition with any one of five Drakensberg *Diascia* species and one eastern Cape species with which it is presently sympatric, or in competition with totally unrelated pollen or nectar plants visited by the same bees. We can only say that the present variation in anther position among *Diascia* species allows coexistence with apparently minimal competition due to interspecific pollen transfer.

Shifts in floral morphology (e.g., pollen placement) as pointed out by Rathcke (1983) are a response to improper/interspecific pollen transfer for species sharing pollinators and will not result in a reduction in the first type of competition (i.e., competition for pollinator visitation). The extent of competition for pollinator visitation among sympatric *Diascia* species is unknown. In most areas visitation rates, as well as the number of bees relative to flowers, appeared quite low (Steiner & Whitehead, unpubl.), yet our data is insufficient to determine whether this apparent limitation of pollinators (a necessary condition for this type of competition) results in a lowered reproductive output for the sympatric *Diascia* species.

We have not examined stigmas of coexisting *Diascia* species to see whether contamination with interspecific pollen occurs despite differences in pollen deposition on the bee. Nor have we progeny tested seed from areas of sympatry to see whether the apparent lack of hybrids in the field (Hilliard & Burtt, 1984; pers. obs.) is due to pre-

TABLE 9. Bees carrying two or more species of *Diascia* pollen.

Rediviva sp.	Location	Elevation (m)	% *Diascia* Pollen	N
R. neliana	The Pudding—Qwaqwa/Royal Natal	2,340	9.3	75
	The Witches—Qwaqwa/Royal Natal	2,600	28.6	7
	The Sentinel—Qwaqwa/Royal Natal	2,760	81.8	22
	Sani Pass, Natal	1,780	6.7	15
	Sani Pass, Natal	2,190–2,260	66.7	6
	Sani Pass, Natal	2,340–2,450	75.0	4
	Qachas Nek, Transkei	1,960	20.0	5
R. sp. nov. 1	Sani Pass, Natal	2,190–2,260	0.0	2
	Sani Pass, Natal	2,340–2,470	33.3	18
	Sani Pass, Natal	2,590	33.3	3
	Naudesnek, E. Cape	2,270	100.0	1
	Carlisleshoek, E. Cape	2,380	50.0	2
	Joubert's Pass, E. Cape	2,140	33.3	3
	Blue Mountain Pass, Lesotho	2,500	18.1	11

cise pollen deposition, to inter-cross incompatibility, or to strong postzygotic selection (cf. Kyhos et al., 1981). Certainly more intensive studies of *Diascia* pollination both within and outside areas of sympatry are warranted.

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STUDIES ON THE REPRODUCTIVE BIOLOGY OF *EUGENIA* L. (MYRTACEAE) IN SOUTHERN AFRICA[1]

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Abstract

Eugenia in southern Africa displays morphological androdioecy. Pollen grains are tricolporate in males and colpate or inaperturate in hermaphrodites, thereby suggesting that the species could be functionally dioecious. The present report includes a general assessment of pollen viability in a number of species and an in-depth study of the reproductive biology in *E. simii*. Pollen grains from males were found to germinate readily whereas those from hermaphrodites were practically inviable. Both types of pollen usually contain a small percentage of aborted grains. Southern African species of *Eugenia* are therefore functionally dioecious, supporting the recent claim that in all known cases of morphological androdioecy functional androdioecy probably does not occur. Neither of the floral types produce nectar but the anthers and pollen grains emit a strong sweet odor. The retention of pollen-producing anthers in females probably serves as a lure to attract pollinators. Honeybees were seen visiting the flowers but other insect species probably also act as pollen vectors. A statistically significant male-biased sex ratio was found in the largest known population of *E. simii*. Casual observations also suggest male-predominant sex ratios in many populations of the other species. No species is gyno-dioecious and no evidence of apomixis was found. Preliminary bagging experiments show that fruit is only produced by bisexual flowers pollinated with grains from male flowers. Sexual dimorphism is rare in Myrtaceae and has not been recorded in *Eugenia* outside Africa. Dioecy in the African species of *Eugenia* may have evolved directly from hermaphroditism, or via androdioecy or gynodioecy. Curiously, this functional dioecy is present in two groups of species which on other grounds do not seem to be closely related.

Résumé

Dans le sud de l'Afrique, *Eugenia* est morphologiquement androdioïque. Les pollens sont tricolporés chez les mâles et colporés ou inaperturés chez les hermaphrodites, ce qui suggère que les espèces peuvent être fonctionellement dioïques. Ce rapport comprend un compte-rendu général sur la variabilité du pollen dans plusieurs espèces et une étude détaillée de la biologie reproductrice de *E. simii*. Les pollens des mâles germinent facilement tandis que ceux des hermaphrodites sont pratiquement non-viables. Les deux types de pollens contiennent habituellement un petit pourcentage de grains avortés. Les espèces indigènes de *Eugenia* sont donc fonctionnellement dioïques et semblent appuyer la thèse récente selon laquelle dans tous les cas connus d'androdioïcie morphologique, l'androdioïcie fonctionelle ne se produit pas. Aucun des deux types floraux ne produit de nectar mais les anthères et les pollens dégagent une odeur douceâtre forte. La rétention d'anthères producteurs de pollen chez les femelles sert probablement à attirer les pollinisateurs. Des abeilles butinent les fleurs mais il y a sans doute d'autres espèces d'insectes qui agissent aussi comme des vecteurs de pollen. Il y a un nombre significatif plus élevé de mâles dans les plus grandes populations connues de *E. simii*. Quelques observations suggèrent également une prédominance de mâles dans de nombreuses populations des autres espèces. Aucune espèce n'est gynodioïque et on n'a pas trouvé de preuves d'apomixis. Des experiences préliminaires démontrent que des fruits sont seulement produits par les fleurs bisexuelles qui ont été pollinisées avec des pollens provenant de fleurs mâles. Le dimorphisme sexuel est un phénomène rare chez les Myrtacées et n'a pas été signalé dans de genre *Eugenia* en dehors de l'Afrique. Dans les espèces africaines d'*Eugenia* la diécie a peut-être évoluée directement des taxons hermaphrodites, ou peut-être en passant par des espèces androdioïques ou gynodioïques. Il est curieux de noter que diécie fonctionnelle se trouve dans deux groupes d'espèces qui sembleraient ne pas être très étroitement liées autrement.

Eugenia is a large pantropical genus of several hundred species concentrated in Central and South America. It is poorly represented in Africa and the rest of the Old World. The small group of African species is of considerable interest in being the only known members of the genus that

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TABLE 1. List of southern African species of *Eugenia* covered by this paper, arranged according to supraspecific group.

Group	Species
X	*E. capensis* (Eckl. & Zeyh.) Sond.
X	*E.* cf. *mossambicensis* Engl.
X	*E. natalitia* Sond.
X	*E. simii* Dümmer
X	*E. umtamvunensis* Van Wyk
Y	*E. albanensis* Sond.
Y	*E. erythrophylla* Strey
Y	*E. pusilla* Engl.
Y	*E. verdoorniae* Van Wyk
Y	*E. woodii* Dümmer
Y	*E. zeyheri* (Harv.) Harv.
Y	*E. zuluensis* Dümmer
Y	*E.* sp. A[a]
Y	*E.* sp. B[a]
Y	*E.* sp. C[a]

[a] Undescribed species; vouchers supplied in Van Wyk & Botha (1984).

display sexual dimorphism, a phenomenon relatively rare in the Myrtaceae.

About 15 species of *Eugenia* are native to southern Africa. These fall into two groups (provisionally referred to as species groups X and Y) delimited by various morphological and anatomical characters (Van Wyk, 1978, 1980a, 1985b; Van Wyk et al., 1980, 1982; Van Wyk & Botha, 1984). Natural populations of all the native species are androdioecious, consisting of plants with either morphologically male or morphologically hermaphrodite flowers. Androdioecy is considered very rare among flowering plants (Lloyd, 1975; Charlesworth & Charlesworth, 1978; Bawa, 1980; Willson, 1983).

In a recent review of androdioecy in seed plants, Charlesworth (1984) argues that, while plant populations do exhibit morphological androdioecy, in all known cases functional androdioecy probably does not occur. These morphologically androdioecious plants are in fact functionally dioecious. Several features of the taxa indicate functional dioecy (Charlesworth, 1984). These include 1 : 1 sex ratios, inaperturate and/or nongerminable pollen in bisexual flowers, and indehiscent anthers. In addition, all probably lack nectar, indicating pollination either by wind or pollen-gathering bees.

The evolution of dioecy has attracted much attention in recent years (e.g., Bawa, 1980, 1984; Ross, 1982). If functional androdioecy is extremely rare, if it occurs at all, then the claims that androdioecy may be an important pathway in the evolution of dioecy (Bawa & Beach, 1981; Ross, 1982) are not valid.

An assessment of the taxonomic significance of pollen morphology in 14 southern African species of *Eugenia* showed that all the investigated species produce strongly dimorphic pollen (Van Wyk & Dedekind, 1985). Pollen grains are tricolporate in males and colpate or inaperturate in hermaphrodites. The lack of ora (endopores) suggests that the grains from hermaphrodites may be inviable (or nearly so), thus rendering the flowers functionally female. This prompted the present study, which includes a general assessment of pollen viability in a number of species and a more detailed study of the biology of sex expression in *E. simii* Dümmer. Our major objective was to determine whether *Eugenia* in southern Africa is functionally androdioecious or, as predicted by Charlesworth (1984) and suggested by pollen morphology, functionally dioecious.

Available information on breeding systems in *Eugenia* (and the Myrtoideae in general) is meager. We suggest that a comparative study of breeding systems in *Eugenia* may provide an understanding of the possible evolution of dioecism via androdioecy in particular. Therefore the present paper also attempts to bring together some evidence and speculations on the reproductive biology of *Eugenia* in southern Africa derived from the scattered literature and casual observations made over several years of fieldwork. Although incomplete, our work is presented with the hope that it may encourage more detailed observations and serve as the basis for intensive future investigation.

MATERIALS AND METHODS

POLLEN VIABILITY

A list of southern African species of *Eugenia* arranged according to their supraspecific group is supplied in Table 1. Pollen viability was determined for both sex forms in *E. capensis, E. natalitia, E. simii, E. woodii,* and *E. zeyheri,* all of which were available from botanical and private gardens in Pretoria. Voucher specimens are housed in the H. G. W. J. Schweickerdt Herbarium (PRU).

The hanging drop technique (Stanley & Linskens, 1974) was adopted for the in vitro pollen germination testing. Distilled water containing 0.01% boric acid and varying sucrose concentra-

tions was used as the basic germination medium. All samples (from one male and one female plant per species) were tested at concentrations of 5, 10, 15, 20 and 30% sucrose. Calcium has been found to promote the growth of pollen tubes in certain groups (Shivanna et al., 1983), and all tests were repeated with calcium added to the basic medium at a concentration of 2×10^{-3} mol/dm^{-3} $Ca(NO_3)_2$.

Pollen was collected shortly after sunrise from newly opened flowers. Samples were taken directly from a dehiscing anther and dusted onto the drop of medium. These were then incubated at 27°C. Observations of germination percentage and tube length were made at regular intervals spread over three days.

Alexander's viability stain (Alexander, 1969) was used for the differential staining of aborted and nonaborted pollen grains. Stainability was assessed in freshly collected pollen samples from the same plants in which pollen germination was tested.

For the examination of pollen tubes in the style, open-pollinated flowers of *Eugenia simii* in which fruit development had just commenced were fixed in FAA. The styles (which persist for some time after flowering) were cleared and softened in 0.8 mol/dm^{-3} NaOH at 60°C for 1 hour, stained with 0.1% water soluble aniline blue in 0.1 N K_3PO_4/ 7 H_2O for at least 10 minutes, squashed in a drop of staining medium and viewed under ultraviolet light (Martin, 1959).

POLLEN RESERVES

For detecting the presence of starch, mature pollen grains from freshly dehisced anthers were squashed in potassium iodide-iodine (IKI) (Johansen, 1940) and examined under the light microscope (Baker & Baker, 1979). The presence of oil droplets (confirmed by staining with Sudan Black B) was also recorded.

ODOR PRODUCTION

To locate the source of odor production, different floral parts were cut off and kept for some time in closed vials. Vials containing anthers with pollen, filaments, petals and remaining receptacle with ovary and calyx lobes were prepared. Accumulated odoriferous substances are easily smelled when a vial is opened. For the location of osmophores fresh flowers were dipped for ±5 hours in a 0.1% solution of neutral-red in water (Vogel, 1962). Care was taken not to bruise floral parts during handling.

FIELD OBSERVATIONS

Field observations and bagging experiments were conducted during October 1984 on *Eugenia simii*, a riverine shrub endemic to southern Natal and Pondoland. This species was selected because of its gregarious habit, fairly regular flowering, and easily accessible flowers. Sex ratios were determined in three populations: one on an island in the Umtamvuna River near Port Edward (UR); a second relatively small population along the Uvongo River near Uvongo (UVR); and a third, the largest known population near the bridge over the Umzimkulwana River in the Oribi Gorge Nature Reserve (OG). In each population over 50% of the individuals were flowering and thus could be sexed. No instances of sexual variation within a plant were observed.

Determination of natural fruit set and bagging experiments to test for self-fertilization and nonpseudogamous apomixis were carried out on plants in the UR population only, because of the relative inaccessibility of the other two populations for long-term experiments. Six individuals (three males and three hermaphrodites) were studied in the UR population. To assess natural fruit set, branches with flowers past anthesis (on males) or with withered styles (on hermaphrodites) were bagged with nylon stocking. Branches with unopened flowers were bagged to test for self-fertilization. Unopened flowers were also emasculated and bagged to test for fruit set indicating nonpseudogamous apomixis. All branches with the various treatments were collected two months later and any maturing fruits and/or abscised flowers were counted.

RESULTS

The suspicion that the southern African species of *Eugenia* are functionally dioecious is supported by the information presented in this paper. We shall subsequently consider the plants with morphologically hermaphrodite flowers as females and refer to their flowers as female flowers.

FLOWERING TIME, INFLORESCENCE STRUCTURE, AND FLORAL MORPHOLOGY

Although odd flowering specimens may be found throughout the year, all the native southern African species of *Eugenia* clearly display a

peak flowering season. *Eugenia capensis* and *E.* cf. *mossambicensis* flower in early summer, *E. verdoorniae* in winter, and the remaining species in spring. Individuals and even whole populations may skip flowering for one or more seasons. This is particularly marked in species of the Y group (Table 1). Drought conditions seem to be a major factor responsible for delayed flowering. New growth and flowering in the rhizomatous geoxylic suffrutex, *E. albanensis,* are promoted by grassland fires (Van Wyk, 1985a). This is probably also the case in *E.* cf. *mossambicensis* and *E. pusilla,* which have a similar habit. Most plants in an area are approximately synchronous in flowering.

Depending on the species, flowers are either solitary, in fascicles, small racemes, or cymules. They are predominantly lateral in position. In group Y species, flowers are carried mainly at the first few nodes of the new season's growth. In group X species the flowers tend to predominate on the previous season's growth and some specimens may be distinctly ramiflorous. Inflorescence structure will be discussed in more detail in a forthcoming paper.

Male plants appear to be more floriferous than females. However, detailed field observations on *Eugenia simii* have shown that some females can be just as floriferous as males. Only plants in flower or fruit can be sexed.

Basic floral construction is similar in all southern African species of *Eugenia.* Drawings and detailed descriptions of male and female flowers are provided in Van Wyk (1979, 1980b, 1982). Flowers of *E. simii* are illustrated in Figures 1 and 2.

Female flowers are actinomorphic with four calyx lobes, four free petals, 10 to numerous free stamens borne on a flat "disc" surrounding the base of the style, an inferior usually bilocular ovary, and a style with a simple or bifid (*E. capensis* and *E.* cf. *mossambicensis*) stigma. Stigmas are of the dry type, as in other Myrtaceae (Heslop-Harrison & Shivanna, 1977). Nectaries are absent. Viewed from above, all floral parts are usually more or less white. Petals are occasionally pinkish colored in individuals of some species. Calyx lobes and the hypanthium (floral tube), the latter not prolonged beyond the summit of the ovary, are green. The stamens are perfectly normal and the flowers appear hermaphroditic.

In male flowers the ovary is rudimentary or sometimes apparently absent. A short stylar protuberance, ca. 1 mm long, and rudimentary ovules are occasionally present. The hypanthium forms a hollow cup and appears less swollen from the outside than in female flowers. Otherwise male floral parts are similar to those of female flowers.

Anthers are similar in male and female flowers, and abundant pollen is shed after the thecae have dehisced longitudinally. Each anther connective has a terminal secretory cavity, a feature typical of the Myrtaceae.

In any one population the stamens in female flowers tend to be slightly fewer and shorter than their male counterparts. For example, in *Eugenia woodii* male flowers have 20–30 stamens and female flowers 10–20 (Van Wyk, 1980b). In *E. verdoorniae* stamen number varies from (14–)16–20(–22) in males and (11–)14–16(–20) in females (Van Wyk, 1979). In *E. erythrophylla* the filaments are 4–5 mm long in male flowers and 3–5 mm long in female flowers (Strey, 1972). Strey also pointed out that the petals in female flowers are somewhat larger than in males. In each southern African species of *Eugenia* the two flower types have approximately the same diameter.

NECTAR AND ODOR PRODUCTION

Male and female flowers do not produce nectar but the anthers and pollen grains emit a strong sweet odor. The intensity of the odor varies between samples and deserves further study. No significant odor was detected in other floral parts.

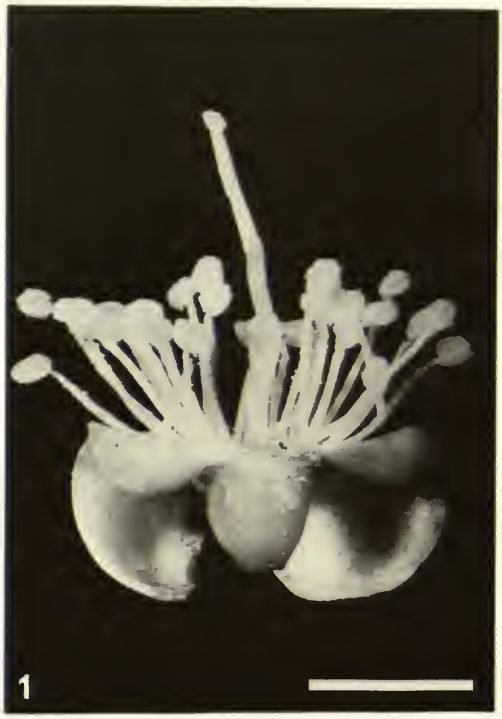
Staining with neutral-red did not reveal any osmophores. Anthers (only if dehisced) and pollen grains stain red but this can be explained by the fact that the stain is effective in areas lacking an intact cuticular membrane. The correlation between the source of the odor and the areas stained is accidental.

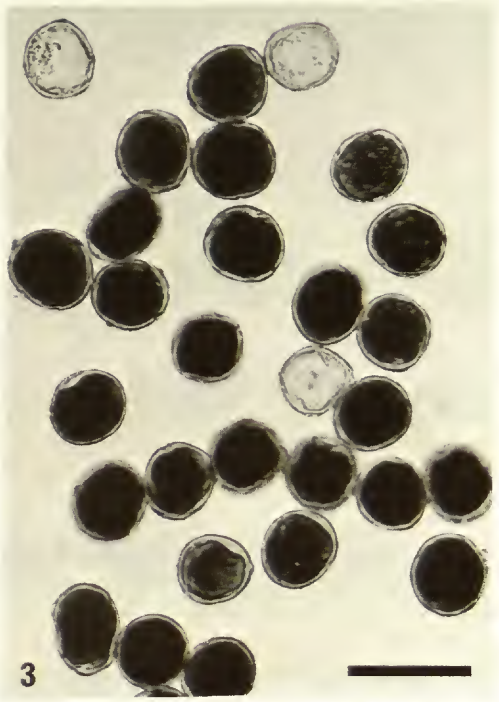
We were unable to demonstrate whether the *original* source of the odor is anther tissue or pollen grains (or perhaps both).

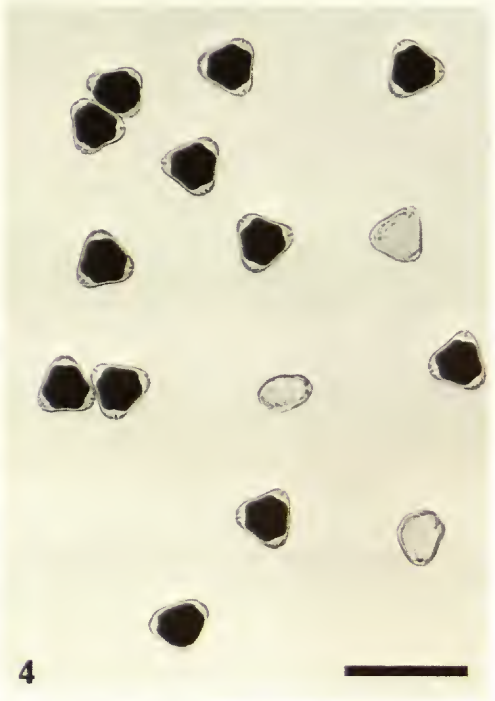
POLLEN MORPHOLOGY

The anthers within a single flower dehisce more or less simultaneously to release the creamish colored pollen grains. Grains are slightly sticky and clump together. Detailed descriptions of the morphology of the dimorphic pollen grains are provided by Van Wyk & Dedekind (1985). Only the outstanding diagnostic characters are summarized below. It is impossible to distinguish species on the basis of palynological features.

Pollen of male flowers is typically myrtaceous and resembles that of hermaphroditic species of *Eugenia.* Grains are free, radially symmetrical, isopolar, oblate to peroblate, (17–)20–25(–30) μm equatorial diameter, triangular, goniotreme and







FIGURES 1–4. Flowers and pollen grains of *Eugenia*. 1, 2. *E. simii*.—1. Structurally hermaphrodite but functionally female flower.—2. Male flower partly dissected to show the cup-shaped hypanthium and absence of a style.—3. *E. natalitia*, stained pollen from female flower showing three aborted grains.—4. *E. woodii*, stained pollen from male flower showing three aborted grains. Scale line = 5 mm in Figures 1, 2; 40 μm in Figures 3, 4.

tricolporate (Fig. 4). Pollen from female flowers deviates considerably from the typical myrtaceous pattern. Grains are free, radially symmetrical, apolar or heteropolar, spheroidal, (22–)28–35(–40) μm diameter, and atreme or colpate (Fig. 3).

In nearly all the samples studied, only one type of pollen morph was present in a particular flower. However, in one or two samples of female flowers we noticed a few apparently normal male-type grains. Occasional female-type grains were also found in a few pollen samples from male flowers. It is likely that at least some of the foreign grains were brought in by pollen vectors (flowers were unbagged). The possibility that male flowers occasionally produce a few female-type pollen grains, and vice versa, nevertheless exists and deserves further investigation.

The staining tests for lipids and starch grains were positive only for lipids. No starch grains were detected. The lipids were in the form of small oil globules.

POLLEN VIABILITY

The use of Alexander's stain showed that all pollen samples contain some aborted grains (Figs. 3, 4). The amount of aborted grains varied from anther to anther but was nearly always less than 20% and in many samples not more than 5%.

Germination results with male pollen (Fig. 6) were rather inconsistent. The germination percentage varied between samples from different anthers in the same flower and between different flowers from the same plant. Whereas pollen from one flower would show almost 90% germination, samples from a neighboring one would fail to germinate. However, such extremes were exceptional. Male pollen germinated in a range of sucrose concentrations from 5 to 30% with perhaps an optimum between 5 and 20%. Pollen from one sample of *Eugenia woodii* even germinated in distilled water! The introduction of calcium to the medium did not improve germination or result in significantly longer tubes. In fact, germination percentages tended to be slightly higher on the basic medium. For most samples germination percentages between 50% and 80% were obtained. The first germinations usually occur within 1–2 hours of commencement of the test and the germination percentage increases rapidly with time, with the maximum percentage normally reached within 24 hours. No pollen tube bursting was observed, even at low sucrose concentrations.

Pollen from female flowers is considered inviable. Only three out of thousands of observed grains showed signs of germination (Fig. 5). These were observed in a single sample of *Eugenia natalitia*. However, the pollen was obtained from an unbagged flower and the possibility of contamination exists. If it was in fact from *Eugenia*, the relatively short tubes produced (compared with length of pollen tubes in males) suggest that they may be unable to reach the ovules.

Cleared styles and stigmas of *Eugenia simii* showed that although abundant female grains are present on the stigma, they do not germinate (Fig. 8). Also present were numerous male grains, the majority of which were found to have germinated. The very large number of fluorescent pollen tubes penetrating the style on their way to the ovules indicate that there must be intense competition among the male pollen grains on a stigma (Fig. 7).

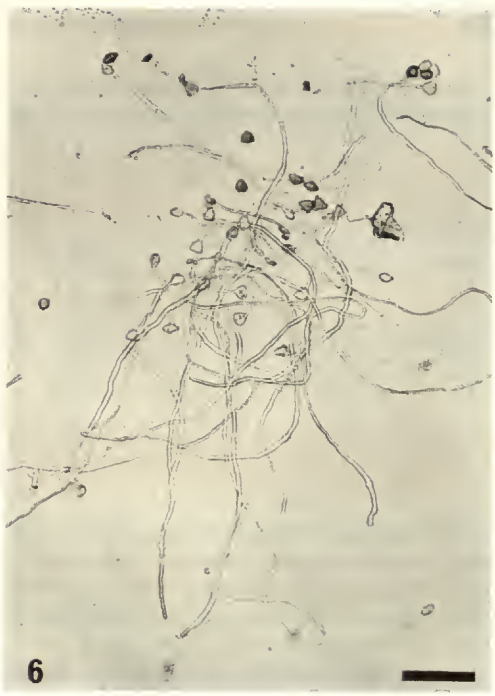
POLLEN VECTORS

There is still some doubt as to the principal pollinators of *Eugenia* in southern Africa. While inspecting populations of *E. simii*, very few potential pollen vectors were noticed. However, the cool, cloudy weather prevailing at the time may have affected insect activity. The only relatively frequent visitors observed on flowering specimens of *Eugenia* growing in Pretoria were honeybees. Honeybees were also seen to be active in natural populations of *E. capensis*. Southern African species of *Eugenia* are provisionally considered to be bee-pollinated.

FRUIT SET AND SEED DISPERSAL

Observations on *Eugenia simii* under natural conditions indicate that only bisexual plants produce fruits. Plants vary considerably in the percentage of fruits set (Table 2), 22–66% of the flowers maturing to fruits. Further studies are needed to determine the possible causes of such variation, including pollinator activity, proximity to male plants, and microhabitat differences.

Cultivated plants of other *Eugenia* species also only produce fruits if they are bisexual. Despite abundant flowering, single female individuals of *E. capensis*, *E. natalitia*, and *E. zeyheri* cultivated in isolation from male plants of the species did not set fruit. Curiously, a few fruits were spotted on two adjacent female plants of *E. woodii* on the campus of the University of Pretoria. The nearest known male plant is in a garden



FIGURES 5–8. Germination of pollen grains in *Eugenia*.—5. *E. natalitia*, in vitro germinating pollen grain from female flower (a very rare phenomenon).—6. *E. woodii*, in vitro germinating pollen grains from male flower. 7, 8. *E. simii*, in vivo pollen germination.—7. Part of a squashed style of an open-pollinated female flower showing numerous pollen tubes with plugs of callose under ultraviolet light.—8. Squashed stigma of open-pollinated female flower showing numerous fluorescent pollen tubes from small grains of male flowers but lack of pollen tubes from the large spherical grains (some arrowed) from female flowers. Scale line = 50 μm in Figure 5; 100 μm in Figures 6–8.

TABLE 2. Fruit set in UR population of *E. simii*.

	Total No. of Flowers Bagged	No. of Fruits	Fruit Set (%)
Female plants			
1	116	72	66
2	45	15	33
3	58	13	22
Male plants			
1	52	0	0
2	45	0	0
3	33	0	0

several kilometers away. Considering the very large number of flowers produced by these females, the five fruits may seem negligible. However, it gives rise to a number of questions that require further study.

Fruits of *Eugenia* in southern Africa are fleshy berries which are nearly always one- (rarely up to three-) seeded. Ripening is usually slightly asynchronous and accompanied by a sequential color change. Seed structure is described by Van Wyk (1980a). Information on seed ontogeny has been discussed by Van Wyk & Botha (1984).

Fruits of group X species usually ripen in a color sequence from green through yellow or reddish orange to dark purple or bluish purple, sometimes even appearing almost black. The pulp of the fruit is whitish and not very tasty. Abundant secretory cavities dot the surface of the fleshy embryo, which has a relatively thin testa.

Fruits of group Y species usually ripen in a color sequence from green through yellow and reddish orange, eventually becoming bright red. The pulp of the fruit is yellowish and tasty. The fleshy embryo is virtually eglandular and has a relatively thick woody testa.

Additional field observations are needed on the mode of seed dispersal. Birds may be the principal agents of dispersal. In forest species ripe fruits are rapidly removed by vervet and samango monkeys (the latter are particularly fond of *Eugenia zuluensis*), baboons, and red squirrels. In species group Y, *E. albanensis* has the smallest habit, being a grassland suffrutex, whereas other species are forest trees, but it produces the largest fruits (up to 50 mm diam.). When ripe, these fruits are often concealed by a dense cover of grass (Van Wyk, 1985a). Dispersal of the relatively large seeds is still unknown.

SEX RATIOS

Results of the sex ratio determination in the three populations of *Eugenia simii* are presented in Table 3. Although the two small populations have a 1 : 1 sex ratio, the largest population in Oribi Gorge has a statistically significant male-biased sex ratio. This is somewhat unexpected given that previous studies of putatively androdioecious genera have shown a 1 : 1 ratio, indicating functional dioecy (Charlesworth, 1984).

Casual observations made by the senior author over several years at various sites indicate that males seemingly tend to outnumber females. This has made it difficult in some species to obtain adequate female flowering material, which displays more taxonomically useful features than male flowers. There is also a paucity of female flowering specimens of some species in herbaria. All the fertile specimens of six species of *Eugenia* in the South African National Herbarium (PRE) are sorted according to sex in Table 4. Specimens collected by the senior author were not taken into account because they are female biased. However, other factors besides a naturally skewed sex ratio may also account for these herbarium statistics (see Discussion).

TESTS FOR SELFING AND NONPSEUDOGAMOUS APOMIXIS ON *EUGENIA SIMII*

A total of 66 bisexual flowers and 48 male flowers were bagged to test for self-fertilization. All flowers abscised without producing fruits. Eleven bisexual flowers and 10 male flowers that were emasculated and bagged also abscised without producing fruit. These results indicate the lack of self-fertilization and, although the sample size is small, also indicate that nonpseudogamous apomixis is not operative. In the field no male plants of any southern African *Eugenia* species have been observed by us to produce fruits.

DISCUSSION

SEXUAL DIMORPHISM IN *EUGENIA* AND SOME OTHER MYRTOIDEAE

Sexual dimorphism in African species of *Eugenia* has generally been overlooked in older works (e.g., Niedenzu, 1893). Lawson (1871) referred to a specimen of *E. calophylloides* with staminate flowers but did not elaborate on the phenomenon. Engler & Von Brehmer (1917) and Engler (1921) distinguished two groups of *Eu-*

TABLE 3. Sex ratios in populations of *E. simii*.

Population	No. of Males	No. of Females	No. Not Flowering	Ratio (female : male)
Oribi Gorge	95	66	43	1 : 1.5*
Uvongo River	7	7	3	1 : 1
Umtamvuna River	21	19	17	1 : 1.1

* $P < 0.05$, $\chi^2 = 5.2$.

genia species in Africa: either with or without the gynoecium sunken into the receptacle. Obviously these groups were based on specimens with male and female flowers, respectively. The suspicion was nevertheless voiced that the group with sunken gynoecia might represent a stage in the reduction of hermaphrodite flowers to unisexual (male) ones (Engler & Von Brehmer, 1917: 334).

Amshoff (1958) noted that the African species of *Eugenia* are "as a rule polygamous or (in *E. tisserantii* Aubréville & Pellegrin according to the collector) dioecious." That flowers of at least some southern African species of *Eugenia* are polygamous was evidently known by authors such as Thonner (1908), Dümmer (1912), and Marloth (1925). More recently, White (1978) noted that all the species of *Eugenia* in the Flora Zambesiaca area display sexual dimorphism.

Amshoff (1958) claimed that if the flowers are polygamous, there may be several male flowers and one or two hermaphroditic flowers in the same fascicle. White (1978) also maintained that hermaphroditic flowers are sometimes accompanied by apparently functionally male flowers. The present study casts doubt on these claims, which we unfortunately were unable to test. During more than 10 years of work on *Eugenia* in southern Africa, the senior author has only once found a male flower among spirit material supposed to be female (then still regarded as hermaphroditic). This led to the description of *E. verdoorniae* as ". . . androdioecious or andromonoecious . . ." (Van Wyk, 1979). Subsequently we have been unable to find male flowers on females and now think that the original observation was based on an accidentally mixed collection. We have also failed to find any female (or morphologically hermaphrodite) flowers in males (gynodioecy). According to Wood (1902), the short-styled flowers in *E. albanensis* represent a developmental stage which is subsequently followed by a lengthening of the style. This was not confirmed by the observations of White (1978). Our observations also find that Wood's observation is wrong.

TABLE 4. Sorting of all fertile collections representing six species of *Eugenia* in the National Herbarium (PRE) according to sexual state.

Species	Number of Specimens		
	Flowering		
	Male	Female	Fruiting
E. albanensis	9	2	1
E. capensis	21	8	17
E. natalitia	18	15	34
E. woodii	13	3	14
E. zeyheri	9	3	5
E. zuluensis	2	0	3

All the southern African species of *Eugenia* are morphologically androdioecious, and there is reason to suspect that this condition occurs in most, if not all, African members of the genus. We have also shown that the species investigated to date are functionally dioecious. This conforms with Charlesworth's (1984) statement that true androdioecy is extremely rare. All the claimed cases of androdioecy reviewed by the latter author appear to involve functional dioecy with females retaining substantial anther vestiges, with the possible exception of *Xerospermum intermedium* (Sapindaceae) (Appanah, 1982). In Myrtaceae, androdioecy has been reported in *Decaspermum* (Niedenzu, 1893; Yampolsky & Yampolsky, 1922), and has recently been confirmed by Kevan & Lack (1985). Kevan & Lack (1985) recorded that pollen of *D. parviflorum* was collected mainly by a variety of bees, mostly *Apis dorsata* and *Nomia* spp.

Significantly, no New World species of *Eugenia* or Old World non-African species of *Eugenia* have been reported to have sexually dimorphic flowers. Dioecy is relatively rare in Myrtaceae, and the family is not listed in a recent compilation of families in which dioecy occurs (Givnish, 1982). However, dioecy can easily be overlooked. Elsewhere in the Myrtoideae *Pimento dioica* (allspice) has a hermaphroditic floral structure but functions as a dioecious species (Chapman & Glasgow, 1961; Chapman, 1964). In this species male and female flowers are similar and even the pollen grains from both floral types are morphologically alike. Germination

tests have, however, shown that female pollen is practically inviable (Chapman, 1964).

FLORAL AND FUNCTIONAL DIOECY

The sexual system in southern African species of *Eugenia* recalls that in dioecious species of *Solanum* (Anderson, 1979; Symon, 1979; Haber & Bawa, 1984); *Decaspermum parviflorum* (Myrtaceae) (Kevan & Lack, 1985); some species of *Tetracera*, and in particular *Saurauia veraguensis* (Dilleniaceae) (Kubitzki & Baretta-Kuipers, 1969; Haber & Bawa, 1984); *Thalictrum polygamum* (Ranunculaceae) (Kaplan & Mulcahy, 1971; Melampy & Hayworth, 1980); and *Actinidia chinensis* (Actinidiaceae) (Schmid, 1978). In these taxa the flowers produce little, if any, nectar and the female flowers produce inviable (often inaperturate) pollen, which obviously serves as a pollinator attractant and/or reward comparable with the phenomenon of feeding anthers in the flowers of some groups (Van der Pijl, 1978; Faegri & Van der Pijl, 1979).

On the basis of their numerous stamens and production of copious pollen, the flowers of *Eugenia* may be classified as typical pollen flowers of the so-called *Papaver* type (cf. Vogel, 1978; Faegri & Van der Pijl, 1979). This particular type of pollen flower also occurs in the Ranunculaceae, Actinidiaceae, and Dilleniaceae (Vogel, 1978), some species of which exhibit functional dioecy comparable to that in *Eugenia*. This suggests that the coevolution with pollen-utilizing insects such as Apidae may lead to a similar form of dioecism in nonrelated groups. The retention of pollen production in female flowers presumably overcomes the expected impediment that the lack of pollinator reward would have on the evolution of dioecy in these groups (Baker, 1984). Baker & Cox (1984) have also pointed out that both male and female flowers must attract the same visitors so that a similar morphological appearance would be advantageous.

FLORAL MORPHOLOGY AND POLLINATOR FORAGING

Beach (1981) has discussed patterns of selective pollinator foraging as one of the possible causative agents in the evolution of dioecy. In this connection Bawa & Opler (1975), Bawa (1974, 1980), and Givnish (1982) have drawn attention to the frequent occurrence in dioecious tree species of small, relatively inconspicuous, white, yellowish or greenish flowers, pollinated by small bees or generalist insects. Bawa & Opler (1975) speculated that in obligately outcrossed species, pollination efficiency may be limited if a hermaphroditic flower's own pollen occupies some of the available space on the stigma. Under such conditions the development of dioecy may reduce the amount of pollen clogging on stigmas that occurs when small insects forage geitonogamously on large crowns. Judged by the large number of pollen tubes in the styles, the presence of many sterile pollen grains on the stigmas of female flowers in *Eugenia* does not seem to be a major impediment to pollination success.

The flowers of Myrtaceae are claimed to be predominantly zoophilous and nectariferous (Johnson & Briggs, 1981). However, a study of *Eugenia, Cleistocalyx*, and *Syzygium* in Ceylon showed that nectarial tissue inside the staminal disc is rare (unfortunately no species were listed) (Kostermans, 1981). An ovarian annular type of nectary is present in some species of *Syzygium* (Schmid, 1972a; see Lack & Kevan, 1984 for details on nectar secretion in *S. syzygioides*). Schmid (1972b) did not report the presence of conspicuous nectaries in flowers of *Eugenia* sensu stricto. We could also not trace any reports on the secretion of nectar in flowers of this genus, an aspect in need of more extensive field observation.

The odor produced by the *Eugenia* pollen grains and/or anthers may play a role in the recognition and detection of the flowers by pollinators. For honeybees particularly, the odor of the pollen grains brought back to the hive may assist in relocation of the flowers. The keen ability of honeybees to differentiate between odors was clearly demonstrated by Von Frisch (1923/24). The possible involvement of some pollinators acting as perfume collectors (Vogel, 1966) also needs to be determined.

Besides nectar, pollen is the most sought-after floral reward (Kevan & Baker, 1983). The present study supports the statement by these authors that lipid-rich pollen grains are particularly common in species where pollen is the only floral reward offered. Baker & Baker (1979) reported that the Myrtaceae may be characterized by starchless mature pollen grains. They also showed that lipids are a major constituent of pollen grains in bee-pollinated flowers. However, a correlation also exists between grain size and the nature of its reserves (Baker & Baker, 1979). The fact that

lipids are common in pollen of Myrtaceae may therefore also be due to the relatively small grains.

POLLEN GERMINATION AND FRUIT DISPERSAL

The variation in germination results obtained with male pollen grains may be due to a desiccation requirement. Elsewhere in the Myrtaceae, Boden (1958) has shown that a period of desiccation is needed for optimal germination of pollen grains in *Eucalyptus viminalis*. It is possible that some of the *Eugenia* pollen samples tested were too fresh.

The color sequence displayed by ripening *Eugenia* fruits strengthens the suspicion that birds may play an important role in the seed dispersal of most species. It has been shown in other groups that bicolored fruiting displays (black and red) significantly enhance fruit removal by frugivorous birds (Mordan-Moore & Willson, 1982; Willson, 1983; Willson & Melampy, 1983). Our findings on *Eugenia* support the observations that dioecy is particularly prevalent among species with fleshy, bird-dispersed fruits (Bawa, 1980; Givnish, 1980, 1982) as well as the association between dioecy and the production of single- or few-seeded fruits (Bawa, 1980; Willson, 1983).

The differences in fruit and particularly seed morphology between species groups X and Y contrast markedly with the similar floral construction and sexual state of the flowers of all the species. This gives rise to several questions, the answers of which may be the subject of considerable speculation. For example, could the present distinctions between groups X and Y perhaps reflect a difference in the particular seed predators or dispersal agents with which two initially closely related taxa have evolved? Could the two groups perhaps represent the end result of two distinct evolutionary lines derived from fairly distantly related ancestral stocks which were subsequently subjected to the same selective pressures (i.e., has there been convergence)? Is the relatively thick testa in species group Y perhaps a measure to counteract the increase in potential dangers which the presence of a tasty pericarp may hold for the embryo? On the other hand, does the less tasty and more tanniniferous pericarp in species group X offer more protection to the embryo, thereby justifying the relatively thin testa? To answer these and other questions more field observations are required to determine the possible selective pressures imposed on fruits and seeds.

SEX RATIOS

Selected data on sex ratios in adult dioecious (mainly morphologically) seed plants are summarized by Willson (1983). The preponderance of males is a common phenomenon which may be caused by factors such as the differential growth of pollen tubes, differential survival, environmentally determined lability of sex expression, and other genetic and environmental factors (Lloyd, 1974; Lloyd & Webb, 1977; Opler & Bawa, 1978; Willson, 1983; Waser, 1984). It would be interesting to see whether the germination of *Eugenia* seeds also yields a significantly male-biased sex ratio. Such a ratio may indicate the possible presence of differential fertilization.

A number of functionally dioecious (morphologically androdioecious) species reviewed by Charlesworth (1984) displayed 1 : 1 sex ratios. Appanah (1982) reported a similar sex ratio in *Xerospermum intermedium,* a structurally androdioecious but functionally dioecious species which may also be functionally androdioecious under certain experimental conditions. However, in this species male trees flower more frequently, resulting in male-biased sex ratios if flowering specimens only are considered. Male-biased sex ratios in *Eugenia* may be due to a similar phenomenon. Casual observations on *Eugenia simii* did not suggest any habitat segregation between males and females. This would be difficult to determine in some of the other species, owing to rarity of individuals in a community. There is a need for more detailed demographic and experimental data on sex ratio variation in *Eugenia.*

The preponderance of male flowering specimens in herbaria may not always indicate a male-biased sex ratio in a natural population. Differential collecting of specimens from more floriferous (and consequently more attractive) male plants could also result in the skewed sex ratio in herbarium collections. This has undoubtedly occurred in *Eugenia,* although females are sometimes just as floriferous as males.

EVOLUTION OF FUNCTIONAL DIOECY IN *EUGENIA*

It has been suggested that dioecism in seed plants has evolved by at least five distinct evolutionary pathways: directly from hermaphroditism, and through androdioecy, gynodioecy, monoecy, and heterostyly (Bawa, 1980; Ross,

1980, 1982). The possible evolutionary pathway to dioecy in the southern African species of *Eugenia* is uncertain. Outside Africa only hermaphrodite flowers are known in *Eugenia*. It has therefore been taken for granted that the hermaphrodite state is the original one from which the dioecious species were derived. Authors have frequently indicated that inbreeding depression is usually necessary for the evolution of dioecy from hermaphroditism (e.g., Charlesworth & Charlesworth, 1978, 1979; also Baker, 1959; Bawa & Opler, 1975). Unfortunately very little seems to be known about inbreeding depression and compatibility in the hermaphroditic species of *Eugenia*. Yet Sobrevila & Arroyo (1982) reported self-incompatibility in a claimed species of *Eugenia* from the Neotropics. It should be stressed that a fair knowledge of breeding systems in *Eugenia* in the whole of Africa and elsewhere is essential to give a proper evaluation of the possible evolutionary pathways involved in the species studied.

On the basis of the present account, evidence for a possible evolutionary pathway from hermaphroditism to dioecy via gynodioecy does not appear particularly strong, but it is still plausible. Although subdioecious plants of this pathway are characterized by well-differentiated females which seldom or never have any pollen (Ross, 1980), a few cases are known in which the females retain nonfunctional stamens (Carlquist, 1966; Young, 1972). If gynodioecy were the pathway in *Eugenia*, then the male flowers would represent hermaphrodite flowers which, through a reduction of seed set, have come to function exclusively as males. Reduction of seed set on hermaphrodites has been described as a gradual process (Lloyd, 1976; Ross, 1980). Therefore one may expect to find an occasional variation in the degree of ovary development in functional males. Although by no means conspicuous, this is indeed the case in *Eugenia* where the ovules and style may be either rudimentary or apparently absent in male flowers. However, the absence of gynodioecy in southern African species of *Eugenia* may be because the evolution of dioecy via unstable gynodioecy has already been attained. Of particular significance may be the reports that both morphologically male and morphologically hermaphrodite flowers are very rarely present on the same plant in some tropical African species of *Eugenia* (Amshoff, 1958; White, 1978). These reports need confirmation because they are apparently based mainly on casual observations in the course of taxonomic revisions. We have, for example, noticed that a morphologically hermaphrodite flower may occasionally lose a style through predation or other damage and could then easily be confused with male flowers, particularly in herbarium specimens.

The sexual state of *Saurauia veraguensis* (Dilleniaceae) recently described by Haber & Bawa (1984) is virtually identical to the condition in southern African species of *Eugenia*. These authors suggest that functional dioecy in *Saurauia* may have evolved via androdioecy or perhaps gynodioecy. The observed rarity of androdioecy (Lloyd, 1975; Charlesworth & Charlesworth, 1978) suggests that it is probably not an important pathway in the evolution of dioecy (Charlesworth, 1984). The rarity or absence of androdioecy has been explained by certain limitations imposed on the transmittance of the necessary controlling genes in a natural hermaphrodite population (Lloyd, 1975; Charlesworth & Charlesworth, 1978; Charlesworth, 1984). However, it has also been speculated that androdioecy could be maintained in outcrossing populations under conditions of a greater pollen production in the males resulting in pollinator mediated sexual selection (Bawa, 1980; Bawa & Beach, 1981; Beach, 1981; Haber & Bawa, 1984).

The presence of fertile pollen in hermaphrodite flowers of *Eugenia* in Africa may lend some support for a possible evolutionary pathway via androdioecy. It is difficult to interpret the significance of the very low numbers of "sterile" grains that germinated in *Saurauia veraguensis* (Haber & Bawa, 1984), *Eugenia* (this study, although origin of grains suspect), *Pimento dioica* (Chapman, 1964), and *Thalictrum polygamum* (Kuhn, 1939; Kaplan & Mulcahy, 1971). Could the germinated grains perhaps represent an incipient stage in the evolution of inviable food grains? The few suspected foreign male-type grains among sterile grains in *Eugenia* obtained from unbagged female flowers could be of considerable importance if it can be shown in future studies that male (fertile) grains may in fact sometimes be produced by females.

In their discussion of dioecy in *Saurauia*, Haber & Bawa (1984) did not mention another plausible pathway, viz. the direct evolution of dioecy from hermaphroditism (Ross, 1982). Charlesworth & Charlesworth (1978) argued on a priori reasoning that the direct evolution of dioecy from hermaphroditism is extremely unlikely because at least two gene mutations (Lewis, 1942; Wes-

tergaard, 1958; Charlesworth, 1984) are deemed necessary. Ross (1982), however, presented some evidence suggesting the existence of a direct pathway without any gynodioecious intermediate stage (see also Bawa, 1980). It is suggested that the latter pathway as well as the ones via gynodioecy and androdioecy could have been involved in the evolution of dioecy in the native species of *Eugenia*. This should be explored further in future studies.

The switch to morphological androdioecism and functional dioecism in both major groups of *Eugenia* in southern Africa is intriguing. Van Wyk & Botha (1984) do not consider species groups X and Y to be closely related and proposed that they may even constitute two separate genera. The distinctness of groups X and Y is also supported by the complete lack of putative hybrids between the two groups, despite the fact that species from both groups often grow together in the field. Evidence presented above indicates that a dioecious sexual state comparable to the one in *Eugenia* also exists among a number of species with pollen flowers in various other families. It therefore appears quite likely that a similar kind of sexual system could have evolved independently in groups X and Y. Such an evolutionary development is likely to have arisen in response to the same or a very similar set of selective pressures. The questions as to the kind of selective pressures involved and why this rather unusual type of functional dioecy in *Eugenia* has only evolved in African species (consisting of two distinct supraspecific groups) offer considerable scope for future investigation.

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TANNINIFEROUS IDIOBLAST PATTERNS AS TAXONOMIC CHARACTERS IN THE GENUS *LITHOPS* N. E. BR. (MESEMBRYANTHEMACEAE)[1]

ROBERT S. WALLACE[2]

ABSTRACT

The relative paucity of useful morphological characters available for species delimitation and identification has perpetuated taxonomic confusion in the genus *Lithops*. Past studies have used leaf and floral characters that are subjectively interpreted, are variable, or are dependent upon the developmental stage of the plant. Fixed, dehydrated, and cleared whole leaves or leaf sections were found to contain idioblastic cells containing condensed tannin. The size of these inclusions and their distribution within the leaves was found to be diagnostic for certain taxa. Four types of upper leaf surface patterns were observed and are stable characters within species groups. The idioblastic tannin inclusions may be classified as having large or small cells relative to the size of the leaf. Eighty-seven taxa were examined, representing 36 species of *Lithops*. The idioblast characters appear to be useful taxonomically at the species level.

RÉSUMÉ

Le manque relatif de caractères morphologiques utiles permettant la délimitation et l'identification des espèces a perpetué une confusion taxonomique dans le genre *Lithops*. Les études précédentes ont utilisé des caractères foliaires et floraux qui sont interprétés subjectivement, sont variables, et dépendent du stade de developpement de la plante. Des cellules idioblastiques contenant des tannins condensés ont été trouvé dans des feuilles entières ou des coupes qui avaient été fixées, déshydratées et éclaircies. La taille de ces inclusions et leur répartition dans les feuilles étaient diagnostiques pour certains taxons. On a observé quatre types de schémas sur la surface supérieur des feuilles qui représentent des caractères stables à l'intérieur des groupes d'espèces. On peut classer les inclusions à tannins idioblastiques comme ayant des cellules relativement grandes ou petites par rapport à la taille de la feuille. Quatre-vingt sept taxons ont été examinés, soit 36 espèces de *Lithops*. Les caractères des idioblastes semblent être utiles d'un point de vue taxonomique au niveau des espèces.

The southern African endemic genus *Lithops* consists of approximately 36 species of highly xeromorphic leaf succulents. These "stone plants" or "vygies" are distributed throughout western and central South Africa and Namibia and are among those Mesembryanthemaceae (Aizoaceae sensu lato) categorized as "mimicry" succulents due to their cryptic coloration and growth habit. The plant body consists of a pair of fleshy leaves, united at their base, forming an obconical cylinder attached to a taproot system. The upper surfaces of the leaf pair may be highly truncate, flattened or convex, with or without clear "window" areas, and are generally pigmented to closely match the surrounding substrate in which they grow.

Previous classifications of the genus have relied primarily on leaf characters, flower color, and seedling morphology. Nel (1946) discussed general attributes of leaf structure including pigmentation patterns, the presence or absense of a "window" (Fenestratae versus Afenestratae), leaf margin, flower, and capsule morphology. In this monograph, the species descriptions included color plates and interpretations of subtle color variations for each species. For many years *Lithops* were identified by comparison with previously published figures and through interpretation of leaf pigmentation patterns, in many cases distinguishing taxa on the color of a particular portion of the leaf. Many of these "color" characters are highly variable and change throughout the development of the plant or within the annual growth cycle. Cole (1975) presented evidence for extreme variation in morphological features of *Lithops*, which may be due to genetic,

[1] I gratefully acknowledge Chester B. Dugdale for his inspiration and early guidance in the study of *Lithops*. The assistance of Desmond T. Cole and Ed Storms is greatly appreciated. This study was funded in part by a research grant from the Cactus and Succulent Society of America.

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habitat, or developmental differences within and between species.

Studies by de Boer & Boom (1964) and later by Fearn (1968) provided some additional characters for species delimitation, but a reliance on color interpretation and other subjective characters is included in their keys and descriptions. To more effectively elucidate infrageneric relationships within the genus *Lithops,* further investigations are required to determine which additional taxonomically useful characters are stable, independent of developmental stage or growth conditions, and do not rely on subjective interpretation.

Anatomical studies on *Lithops* by Dugdale (1966, 1968) disclosed the presence of relatively large idioblastic cells located within the leaf parenchyma. He reported that condensed tannin inclusions found within the idioblastic cells are easily visible in fixed, dehydrated, and cleared leaf tissues, and occur as dark, "reddish-colored bodies" that are "scattered among the parenchyma cells." The tannin inclusions are also visible when the old leaf withers and dries during the annual new leaf development cycle. These inclusions appear as dark amorphous or crystalline masses within the dried leaf remains. In a survey of 25 species representing 15 genera of Mesembryanthemaceae (Dugdale, 1971), it was concluded that tanniniferous idioblasts occur frequently within the leaf tissues of members of this family. He also found that in the genus *Lithops* the patterns of these condensed tannin inclusions are invariant within a species group. Dugdale proposed that these patterns may be diagnostic for particular taxa. This would therefore add another nonsubjective character to those used in species delimitation.

This study examines the taxonomic usefulness of idioblast patterns in the genus *Lithops* and compares controversial taxa included in the systems of Fearn (1968, 1981) and Cole (1973a) using data derived from idioblast pattern interpretation.

Materials and Methods

Leaves of mature plants (three years or older) supplied by Ed Storms (Azle, Texas) and grown from true, field-collected seed supplied by Desmond T. Cole (Emmarentia, Transvaal, South Africa) were used. Whole leaves or leaf sections were excised from the plants following flowering to ensure developmental maturity and standardization of developmental stage. The leaf tissues were then fixed in standard formalin–acetic acid–ethanol (FAA) fixative (Johanson, 1940) or in Dugdale's phosphomolybdic acid fixative (Dugdale, 1971), the latter causing less shrinkage. The tissues were dehydrated through a graded series of ethanol : tertiary butyl alcohol (TBA) to absolute TBA, cleared initially in xylene for 24–48 hours, and placed in pure methyl salicylate (MS), which improved visualization of the condensed tannin inclusions. The tissues were stored in MS in glass vials.

To refer to *Lithops* species and varieties, the system of Cole (1973a) is used throughout this study and each taxon is accompanied by a "C" number, which refers to Cole's collection number. All taxa included in his 1973 treatment are examined, with the exceptions of *L. steineckeana* (unavailable and of questionable status) and *L. elevata* (Cole, 1982) and the addition of *L. naureeniae,* which has since been published (Cole, 1980). Leaves were examined for the presence of condensed tannin inclusions and scored according to the relative size of the inclusions (large or small), the distribution of the inclusions within the leaf (top only, sides only, top and sides, central parenchyma), and the pattern formed by the inclusions when the leaf is viewed from the top.

Results and Discussion

General

It was found that condensed tannin idioblast inclusions occurred in all *Lithops* taxa examined (Table 1). Dugdale (1971) found only occasional idioblasts in *L. hallii* and *L. salicola,* but my study revealed small idioblasts restricted to the top of the plant along the adaxial margin (Fig. 2C) consistently in all specimens examined of these two species. Certain specimens having low numbers of inclusions (e.g., *L. olivacea* and *L. pseudotruncatella* var. *volkii*) are still considered to have patterns diagnostic for their particular species group.

Idioblast Size

Two size classes of idioblastic inclusions were arbitrarily assigned. Large inclusions are usually very dark, red, or brownish in color, have di-

TABLE 1. Relative sizes, distribution, and patterns formed by idioblast inclusions for 87 varieties of *Lithops*, represented in 36 species. The system of Cole (1973a) is used to refer to taxa. Numbers following the species or variety are collection numbers of D. T. Cole.

Taxon*	Size[a]		Distribution[b]				Top Pattern[c]					Pattern Designation
	S	L	T	TS	S	CP	Ia	Ib	II	III	IV	
L. aucampieae												
var. *aucampieae* C-172	X		X					X				Ib.T.sm
var. *euniceae* C-48		X	X							(X)	X	IV.T.lg
var. *fluminalis* C-54	X		X							(X)	X	IV.T.sm
var. *koelemanii* C-16		X	X					X				Ib.T.lg
L. bella												
var. *bella* C-108		X	X	(X)			X				(X)	Ia.T.lg
var. *eberlanzii* C-82		X		X							X	IV.TS.lg
L. bromfieldii												
var. *bromfieldii* C-40		X	X	(X)			X					Ia.T.lg
var. *glaudinae* C-116		X	X				X					Ia.T.lg
var. *insularis* C-57		X	X					X				Ib.T.lg
var. *mennellii* C-44		X	X					X				Ib.T.lg
L. comptonii												
var. *comptonii* C-125	X			X			X					Ia.TS.sm
var. *weberi* C-126	X			X			X					Ia.TS.sm
L. dinteri												
var. *brevis* C-84		X		X							X	IV.TS.lg
var. *dinteri* C-206		X		X							X	IV.TS.lg
var. *frederici* C-180		X		X							X	IV.TS.lg
var. *multipunctata* C-181		X		X							X	IV.TS.lg
L. divergens												
var. *amethystina* C-270	X				X					X		III.S.sm
var. *divergens* C-269	X				X					X		III.S.sm
L. dorotheae C-124		X		X							X	IV.TS.lg
L. erniana												
var. *aiaisensis* C-224		X		X							X	IV.TS.lg
var. *erniana* C-209		X		X							X	IV.TS.lg
var. *witzputzensis* C-149		X		X							X	IV.TS.lg
L. francisci C-140		X		X			X					Ia.TS.lg
L. fulleri												
var. *brunnea* C-179		X			X					X		III.S.lg
var. *fulleri* C-24		X		(X)	X					X		III.S.lg
var. *rouxii* C-217		X		(X)	X					X		III.S.lg
L. fulviceps												
var. *fulviceps* C-266		X	X				X					Ia.T.lg
var. *lactinea* C-222		X	X				X					Ia.T.lg
L. gesinae												
var. *annae* C-78		X	X				X	(X)				Ia.T.lg
var. *gesinae* C-207		X		X		(X)	X					Ia.TS.lg
L. gracilidelineata												
var. *gracilidelineata* C-262	X		X				X					Ia.T.sm
var. *waldronae* C-189	X		X				X					Ia.T.sm

TABLE 1. Continued.

Taxon*	Size[a]		Distribution[b]				Top Pattern[c]					Pattern Designation
	S	L	T	TS	S	CP	Ia	Ib	II	III	IV	
L. hallii												
var. *hallii* C-22	X		X						X	(X)		II/III.T.sm
var. *ochracea* C-98	X	(X)	X							X		III.T.sm
L. helmutii C-271	X				X					X		III.S.sm
L. herrei												
var. *geyeri* C-274	X			(X)	X					X		III.S.sm
var. *herrei* C-234	X				X					X		III.S.sm
L. julii C-64	X			X							X	IV.TS.sm
L. karasmontana												
var. *lericheana* C-267	X		X	(X)							X	IV.T.sm
var. *karasmontana* C-225	X		X								X	IV.T.sm
var. *tischeri* C-182	X		X								X	IV.T.sm
L. lesliei												
var. *hornii* C-15	X	(X)	X				X					Ia.T.sm
var. *lesliei* C-10	X		X				X					Ia.T.sm
var. *mariae* C-141	X		X				X					Ia.T.sm
var. *minor* C-6	X		X				X					Ia.T.sm
var. *rubrobrunnea* C-204	X		X				X					Ia.T.sm
var. *venteri* C-1	X		X				X					Ia.T.sm
L. localis C-133	X	(X)	X								X	IV.T.sm
L. marmorata												
var. *elisae* C-251	X			(X)	X						X	IV.S.sm
var. *marmorata* C-260	X			(X)	X					(X)	X	IV.S.sm
L. meyeri C-212	X				X					X		III.S.sm
L. naureeniae C-304	X				X						X	IV.S.sm
L. olivacea C-162B	X		X					X				Ib.T.sm
L. optica C-275	(X)	X		X						X	(X)	III.TS.lg
L. otzeniana C-128	X			X	(X)					X	(X)	III.TS.sm
L. pseudotruncatella												
var. *archerae* C-104		X	X				X					Ia.T.lg
var. *dendritica* C-73	X		X				X					Ia.T.sm
var. *edithae* C-97	X		X					X				Ib.T.sm
var. *elisabethae* C-187	X		X					X				Ib.T.sm
var. *pseudotruncatella* C-67	X		X					X				Ib.T.sm
var. *volkii* C-69	X		X					X				Ib.T.sm
L. ruschiorum												
var. *lineata* C-314	X	(X)	X	(X)			X					Ia.T.sm
var. *ruschiorum* C-242	X	(X)		X			X					Ia.TS.sm
L. salicola C-49	X		X						X			II.T.sm
L. schwantesii												
var. *christinae* C-210		X	X				X					Ia.T.lg
var. *gebseri* C-165		X	X				X					Ia.T.lg
var. *kunjasensis* C-248		X	X				X					Ia.T.lg
var. *marthae* C-249		X	X				X	(X)				Ia.T.lg
var. *rugosa* C-192		X	X				X					Ia.T.lg
var. *schwantesii* C-191		X	X				X	(X)				Ia/b.T.lg
var. *urikosensis* C-83		X	X				X					Ia.T.lg

TABLE 1. Continued.

Taxon*	Size[a]		Distribution[b]				Top Pattern[c]					Pattern Designation
	S	L	T	TS	S	CP	Ia	Ib	II	III	IV	
L. turbiniformis												
var. *dabneri* C-13	X		X				X					Ia.T.sm
var. *elephina* C-92	X	(X)	X				X					Ia.T.sm
var. *lutea* C-38	X	(X)	X				X	(X)				Ia.T.sm
var. *marginata* C-35	X		X					X				Ib.T.sm
var. *subfenestrata* C-21	X		X					X				Ib.T.sm
var. *susannae* C-91	X		X					X				Ib.T.sm
var. *turbiniformis* C-142-B, C-23	X		X					X				Ib.T.sm
L. vallis-mariae												
var. *groendraaiensis* C-244	X		X					X				Ib.T.sm
var. *vallis-mariae* C-282	X		X					X			(X)	Ib.T.sm
L. verruculosa												
var. *glabra* C-160		X		X		X	X					Ia.TS/CP.lg
var. *verruculosa* C-159		X		X		X	X					Ia.TS/CP.lg
L. villetii												
var. *deboeri* C-230A	X		X								X	IV.T.sm
var. *kennedyi* C-200A	X		X							X	(X)	III.T.sm
var. *villetii* C-195	(X)	X	X	(X)							X	IV.T.lg
L. viridis C-127	X			X			X				(X)	Ia.T.sm
L. werneri C-188	X		X					X				Ib.T.sm

[a] Size: S = small idioblast inclusions; L = large idioblast inclusions.
[b] Distribution: T = top; TS = top and sides; S = sides; CP = central parenchyma.
[c] Pattern: Ia = uniform distribution, dense; Ib = uniform distribution, spaced; II = adaxial margin distribution; III = ad- and abaxial margin distribution; IV = ad- and abaxial top distribution with scattered central inclusions.
* Items in parentheses indicate occasional occurrence of particular character.

ameters from approximately 0.5–1.5 mm, and are strikingly obvious in cleared leaf tissues. Small inclusions appear as sandlike grains, often densely arranged within the parenchyma, are generally less than 0.5 mm in diameter, and are more difficult to observe within the leaves.

DISTRIBUTION WITHIN THE LEAF

The condensed tannin inclusions are restricted to the top of the truncate portion of the leaf in 21 of the 36 species studied. Approximately eight species had idioblast distributions in both the top and sides of the leaves. Seven species showed distributions restricted to the sides or abaxial periphery of the leaf. Figure 1 is a schematic representation of the distribution of the inclusions within the leaves. A few species or varieties displayed overlap in these categories. In one species (*L. verruculosa*) idioblasts were found in all portions of the leaf, including the clear, central parenchyma.

IDIOBLAST PATTERNS

In all cases, patterns formed by the idioblastic inclusions when viewed from the upper surface of the leaf pair were found to be bilaterally symmetrical in each of the leaves with respect to the cleft between them. Thus, the pattern found in a single leaf would adequately represent its "copy" in the other leaf. Four basic patterns of idioblast distribution were found (Fig. 2). The Type I pattern (Fig. 3a) is a uniform distribution of idioblastic inclusions across the whole upper leaf surface. The relative density of the distribution of these inclusions has been arbitrarily designated as dense (Type Ia, Fig. 2A) or spaced (Type Ib, Fig. 2B), the latter having inclusions spaced greater than 2–3 mean idioblast diameters between them. The Type II pattern (Fig. 2C) has idioblasts only along the adaxial margins of the leaf pair (Fig. 3b). Type III patterns (Fig. 2D) are those with a "centrifugal" distribution of inclusions about the adaxial and abaxial periphery, with an "open" central region (Fig. 3c). The Type

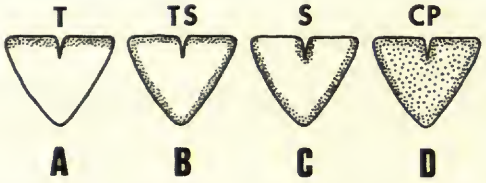

FIGURE 1. Schematic representation of tanniniferous idioblast inclusions in the leaves of *Lithops*. Longitudinal section of the leaf pair is shown, perpendicular to the cleft.—A. Distribution restricted to the top (T) only.—B. Distribution in both the top and sides (TS).—C. Distribution restricted to the sides (S) of the leaves only.—D. Idioblasts distributed in the clear, central parenchyma (CP).

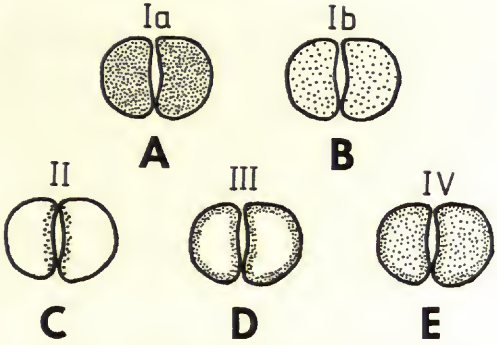

FIGURE 2. Patterns formed by tanniniferous idioblast inclusions in *Lithops* leaves when viewed from the top surface.—A. Type Ia pattern with dense, uniform distribution across the surface.—B. Type Ib pattern having uniform distribution, but spaced more than in Type Ia.—C. Type II pattern with idioblasts at the adaxial margin of the leaf.—D. Type III pattern with distribution of idioblasts in both the adaxial and abaxial leaf margins, with a clear, central region.—E. Type IV pattern, similar to Type III, but with scattered idioblasts in the central region.

IV pattern (Fig. 2E) is similar to the Type III pattern, with the addition of scattered central inclusions, often randomly arranged or occasionally in a reticulate pattern within this central region (Fig. 3d).

Each taxon (species or variety) may be assigned an encoded designation combining idioblast pattern, distribution, and relative cell size to facilitate comparison and discussion. For example, *Lithops fulviceps,* which has large idioblasts densely arranged and restricted to the top of the plant, would carry the designation Ia.T.lg, while *L. divergens,* having small idioblasts with a Type III pattern and distribution restricted to the sides, would be encoded III.S.sm. The designations for each taxon are included in Table 1.

PHYLOGENETIC CORRELATIONS

A correlation was found between plants having a strongly bifurcate morphology (*L. divergens, L. helmutii, L. meyeri, L. naureeniae*) and Type III and IV patterns of small cells with distributions about the sides only. Plants with markedly flattened (truncate) leaves (*L. fulviceps, L. gracilidelineata, L. pseudotruncatella, L. schwantesii*) tended to have inclusions restricted to the top of the leaf and arranged in a Type I pattern. The more "rounded" species having convex leaf surfaces (*L. comptonii, L. dorotheae, L. francisci, L. ruschiorum, L. viridis*) were among those possessing top and side distribution. No correlation between idioblast pattern or distribution and flower color was observed, with the notable exception of *L. verruculosa.* This species was the only one having (very large and dense) idioblasts within the central parenchyma as well as within the top and sides. It is also the only species exhibiting a variable range of flower colors from yellowish-peach to orange-cream, quite different than the more usual yellow or white flowers of all other species. While these new data present

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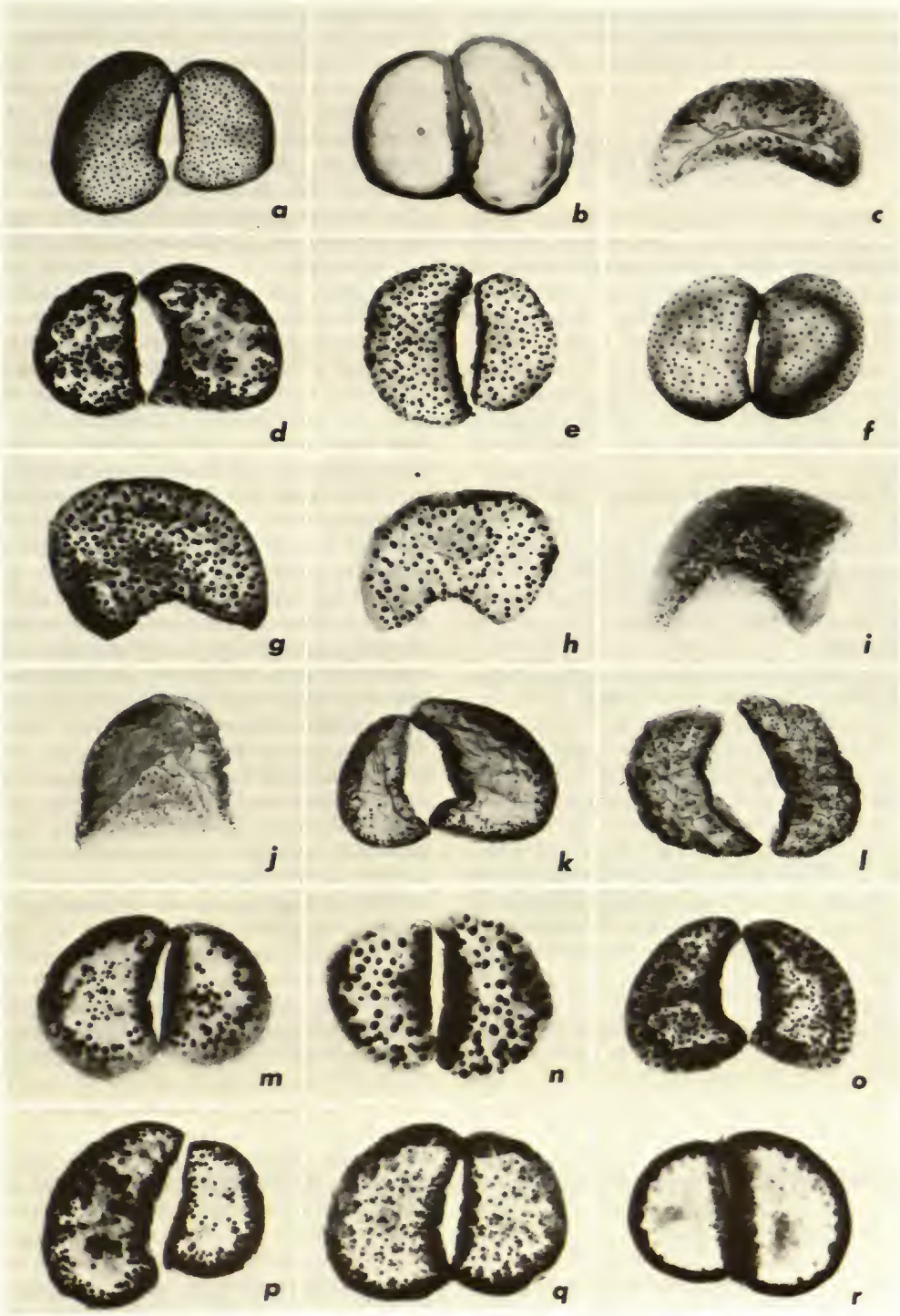
FIGURE 3. Whole sections of upper leaf tips of selected *Lithops* species. The tissues were fixed, dehydrated, cleared, and photographed with transmitted light. Idioblastic inclusions appear as dark bodies within the cleared tissues of the leaf. Figures are not to scale; magnifications not equal.—a. *Lithops pseudotruncatella* var. *elisabethae* C-187.—b. *L. salicola* C-49.—c. *L. meyeri* C-212.—d. *L. erniana* var. *aiaisensis* C-224.—e. *L. pseudotruncatella* var. *archerae* C-104.—f. *L. pseudotruncatella* C-67.—g. *L. bromfieldii* var. *glaudinae* C-116.—h. *L. bromfieldii* var. *insularis* C-57.—i. *L. comptonii* C-125.—j. *L. divergens* var. *amethystina* C-270.—k. *L. marmorata* C-260.—l. *L. marmorata* var. *elisae* C-251.—m. *L. dinteri* C-206.—n. *L. schwantesii* var. *marthae* C-249.—o. *L. schwantesii* C-191.—p. *L. villetii* var. *villetii* C-195.—q. *L. villetii* var. *deboeri* C-230A.—r. *L. villetii* var. *kennedyi* C-200A.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further evidence for the uniqueness of *L. verruculosa*, additional characters must be examined to ascertain how this species is related to the others.

TAXONOMIC USEFULNESS OF IDIOBLAST CHARACTERS

The application of data derived from the study of idioblast patterns is perhaps best suited to resolving problems in delimitation of taxa at the species level. The size, distribution, and the pattern made by idioblasts within a species group appears to be a stable character, useful for direct comparison of taxa in question. The following discussion compares the classifications of Fearn (1968, 1981) and Cole (1973a) with regard to controversial taxa between each of these two systems.

Inclusion of *Lithops archerae* de Boer (Fig. 3e) in *L. pseudotruncatella* (Berg.) N. E. Br. (Fig. 3f) as a variety appears to be valid, however var. *archerae* appears to be the most different variety, with closest affinity to var. *dendritica*, both having denser idioblast distributions than the other varieties.

The placement of *Lithops eberlanzii* (Dinter & Schwantes) N. E. Br. in *L. bella* N. E. Br. as a variety by de Boer was adopted by both Fearn and Cole, but recently Cole has reassigned specific status to this taxon (pers. comm.). Idioblast data support this change, since *L. bella* has Type Ia.T.lg idioblasts and *L. eberlanzii* has Type IV.TS.lg idioblasts. Further controversy within the *L. bella-karasmontana* complex includes the placement of *L. lericheana* (Dinter et Schwantes) N. E. Br. within either of these two species. Idioblast data support Cole's placement of *lericheana* into *L. karasmontana*, both taxa possessing a Type IV.T.sm pattern.

Fearn recognizes *Lithops glaudinae* de Boer (Fig. 3g), while Cole treats it as a variety of *L. bromfieldii* L. Bol. (Fig. 3h). Both taxa have Type I.T.lg idioblast patterns and upon clearing are often indistiguishable, except perhaps in leaf shape. This supports *L. bromfieldii* var. *glaudinae* (de Boer) Cole as proper status for this variety.

The inclusion of *Lithops divergens* L. Bol. in *L. comptonii* L. Bol. (Fig. 3i) by Fearn is not supported by idioblast pattern. *Lithops divergens* (Fig. 3j) has a Type III.S.sm pattern; the *L. comptonii* pattern is Type Ia.TS.sm. The assignment of *L. weberi* Nel to *L. otzeniana* var. *weberi* (Nel) Fearn is also not supported, *L. otzeniana* having a Type III.TS.sm pattern. *Lithops weberi* has the same Ia.TS.sm pattern as *L. comptonii*, and Cole's placement of it as *L. comptonii* var. *weberi* (Nel) Cole seems justified. Additional data are needed to support Fearn's placement of *L. viridis* H. Luckh. in *L. comptonii*. Further investigation is warranted, since the idioblast pattern of *L. viridis* (Type Ia.T.sm) differs from *L. comptonii* only in that the latter has idioblasts along the sides as well as the top.

The affinities of *Lithops marthae* Loesch et Tisch. (Fig. 3n) to either *L. dinteri* Schwantes or *L. schwantesii* Dinter have been questioned, and placement of the species as a variety of *L. schwantesii* by Cole (1973b) is generally supported by idioblast pattern characters. Both of these taxa have Type Ia.T.lg patterns, while *L. dinteri* (Fig. 3m) and all of its varieties have a Type IV.TS.lg pattern. Thus *L. schwantesii* var. *marthae* (Loesch et Tisch.) Cole is an appropriate combination, although this variety may be related to *L. dinteri* as Fearn suggests. Fearn also supports the hypothesis that *L. dinteri* and *L. dorotheae* Nel are closely related, based on crossing experiments. *Lithops dorotheae* also has a Type IV.TS.lg idioblast pattern; this further suggests a possible close phylogenetic relatedness between these two species.

Based strictly on idioblast pattern, the inclusion of both varieties of *Lithops gesinae* (var. *annae* de Boer and var. *gesinae* de Boer) in *L. francisci* (Dinter et Schwantes) N. E. Br. by Fearn cannot be disputed, since both possess a Type Ia.TS.lg pattern. Further data are necessary to determine if *L. gesinae* warrants separate specific status.

The species complex including *Lithops fulleri* N. E. Br., *L. julii* (Dinter et Schwantes) N. E. Br., and *L. hallii* de Boer has undergone scrutiny of several researchers. Fearn includes *L. fulleri* as a subspecies of *L. julii* and regards *L. hallii* as a hybrid between *L. salicola* and one or more varieties of *L. fulleri*. The idioblast pattern of *L. hallii* does seem to be intermediate between *L. salicola* and varieties of *L. fulleri*. While the hybrid status of *hallii* cannot be definitively supported or refuted with idioblast data, a distinction between *L. julii* (Type IV.TS.sm) and *L. fulleri* (Type III.S.lg) may be made and is supportive of the retention of specific status for *L. fulleri*.

Lithops elisae de Boer (Fig. 3l) has been assigned varietal status by Cole as *L. marmorata*

var. *elisae* (de Boer) Cole, while Fearn retains it as a species. Both *L. elisae* and *L. marmorata* (Fig. 3k) have Type IV.S.sm idioblast patterns, which is consistent with Cole's treatment.

Placement of *L. gracilidelineata* Dinter as a variety of *L. pseudotruncatella* (Berg.) N. E. Br. by Fearn is supported by idioblast data, both taxa having Type I.T.sm patterns. Further data is necessary to substantiate inclusion or exclusion of *gracilidelineata* into the variable species group of *L. pseudotruncatella.*

Idioblast distribution in the varieties of *Lithops villetii* L. Bol. (Fig. 3p) largely supports the inclusion of *L. deboeri* Schwantes (Fig. 3q) as a variety of *L. villetii.* Although similar in external morphology, the idioblast pattern of *L. villetii* var. *kennedyi* (de Boer) Cole (Fig. 3r) is a Type III.T.sm pattern and quite distinct from the other two varieties, var. *deboeri* and var. *villetii,* which have Type IV.T.sm and IV.T.lg patterns, respectively. Jump (1981) found that var. *deboeri* and var. *kennedyi* resembled each other more than they resembled var. *villetii* in seed characters. In this study, var. *villetii* was found to have much larger idioblast cells than either of the other two varieties but shared the same Type IV pattern with var. *deboeri.* The relationships of these three taxa to each other is not clear. Additional data are needed to help determine their relationships and the appropriate status for each.

It must be stressed that although idioblast patterns may provide an additional, relatively stable diagnostic character for species determination, decisions based on a single character will provide little data toward developing a phylogenetically-derived classification system that accurately assesses the integrity of evolutionary species units. The decisions involved in determining the phylogenetic and taxonomic relatedness of *Lithops* species and varieties should be made using a standard set of characters that do not rely on subjective interpretation and that are relatively independent of developmental and habitat-related variation. Through multidisciplinary biosystematic studies, the shroud of taxonomic confusion that has plagued *Lithops* in the past will be removed and a more thorough understanding of the relationships between the species of the "stone plants" will be possible.

Note added in proof. The idioblast pattern of *Lithops steineckeana* Tisch. (Fritz F-240) was determined to be Ia.T.sm, similar to that of one of its putative parents, *L. pseudotruncatella.*

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FLORE DE LA CÔTE D'IVOIRE: ÉTUDE DESCRIPTIVE ET BIOGÉOGRAPHIQUE, AVEC QUELQUES NOTES ETHNOBOTANIQUES[1]

LAURENT AKÉ ASSI[2]

RÉSUMÉ

Afin de contribuer à l'accroissement et à l'approfondissement des connaissances sur la végétation de l'Afrique de l'ouest en général, et sur celle de la Côte d'Ivoire en particulier, j'ai entrepris, depuis plus d'un quart de siècle, des recherches floristiques, encouragé par Georges Mangenot, alors Professeur à la Faculté des Sciences de l'Université de Paris, et Directeur du Centre ORSTOM d'Adiopodoumé, et les autorités gouvernementales et scientifiques de mon pays. Les résultats de mes investigations, effectuées dans tous les biotopes, aussi bien en Côte d'Ivoire que dans les pays limitrophes, et qui ont permis la réalisation de ma thèse de Doctorat d'État, peuvent se résumer en cinq points:

(1) La flore de la Côte d'Ivoire compte 3.660 espèces de plantes vasculaires, réparties en 1.218 genres et 192 familles.

(2) L'originalité de la flore est due à un endémisme important aux niveaux de la famille, du genre, et de l'espèce.

(3) Le rapport du nombre des espèces au nombre des genres est de 3.005, eu égard à de nombreux genres multispécifiques dans certaines familles.

(4) Cette étude a montré que deux flores, numériquement semblables, peuvent présenter des différences considérables.

(5) Au sein de la flore ivoirienne, j'ai distingué deux catégories d'espèces d'inégale importance: les espèces pluricontinentales, moins nombreuses, et les espèces strictement africaines, qui représentent plus de 82% des plantes recensées dans le pays.

ABSTRACT

In order to increase our understanding of the vegetation of West Africa and the Ivory Coast in particular, I have conducted floristic research for the last 25 years, following the suggestions of Georges Mangenot, then Professor at the Faculté des Sciences de l'Université de Paris and Director of the ORSTOM Center in Adiopodoume, as well as the governmental and scientific authorities of my country. The results of my work, covering all the biotypes in Ivory Coast and surrounding countries, and which resulted in my doctoral thesis, may be summarized in five points:

(1) The flora of the Ivory Coast comprises 3,660 species of vascular plants in 1,218 genera and 192 families.

(2) The distinctness of the flora results from high endemism at the family, genus, and species level.

(3) The ratio of species to genera is 3.005, due to numerous multispecific genera in certain families.

(4) This study indicates that two floras that are similar in number of species may show considerable differences.

(5) Within the flora of the Ivory Coast, I distinguish two numerically different groups of species: those occurring on several continents, which are fewer in number; and those that are strictly African, which represent over 82% of the known species.

Dans le domaine de la connaissance floristique de l'Afrique de l'Ouest, la Côte d'Ivoire est l'un des pays les mieux connus: en effet, depuis plus de trois quarts de siècle, d'éminents botanistes explorent et étudient les différentes régions du pays, dans tous les domaines de la botanique. Les travaux des uns et des autres ont permis une parfaite connaissance taxonomique de la flore. Mais, il reste à écrire une flore générale de ce pays et à caractériser cette flore du point de vue biogéographique; un travail d'ensemble de cette sorte importe d'autant plus qu'il doit être un outil d'identification exacte des espèces, mis à la disposition de tous et pouvant servir, même dans les dispositions qui seront prises, pour l'aménagement du territoire et pour la protection de la nature.

Aussi, les documents que je présente constituent-ils, en quelque sorte, un prodrome d'une flore pratique de la Côte d'Ivoire, oeuvre que je souhaiterais mener à bien. Depuis plus de 25 ans, j'ai, chaque année, réalisé, dans toutes les régions

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de notre pays, un inventaire approfondi de la flore, au cours de tournées répétées, en toutes saisons. J'ai porté autant d'intérêt aux forêts ombrophiles, autrefois si majestueuse, qu'aux forêts claires et aux savanes de la région septentrionale, soudano-zambézienne, du pays.

Ce travail, essentiellement floristique, a été rendu possible grâce à ces années de recherches sur le terrain, complétées par un important travail dans de riches herbiers étrangers (notamment en France, en Grande Bretagne, et en Belgique). J'ai, moi-même, créé l'Herbier du Centre-O.R.S.T.O.M. d'Adiopodoumé ainsi que celui de l'Université d'Abidjan, entouré d'un jardin botanique, où je m'efforce de conserver les espèces rares et en danger d'extinction, de la flore ivoirienne.

Les nombreux voyages que j'ai eu la bonne fortune d'accomplir, tant en Europe que dans d'autres régions tropicales, m'ont permis de mieux comprendre et de situer, dans un cadre général, la flore, relativement pauvre, de l'Afrique Occidentale et, en particulier, celle de la Côte d'Ivoire.

Présentation du Travail

Ce travail comprend trois parties.

A. Une liste commentée de toutes les espèces d'angiospermes recensées en Côte d'Ivoire. Cette liste a pour objet de donner une idée précise, une vision complète, de la flore angiospermienne et de mettre en évidence les caractères fondamentaux de chaque famille. C'est un tableau complet qui comprend pour chaque famille plurispécifique, qu'elle soit plurigénérique ou unigénérique, cinq volets successifs.

1. Le premier volet est l'inventaire des espèces spontanées.

2. Les tableaux du deuxième volet ont pour objet de préciser la chorologie, pour chaque espèce, d'abord dans le cadre mondial, puis dans celui de l'Afrique.

3. Dans le troisième volet sont rassemblées des informations concernant les caractères présentés par chaque espèce dans un milieu naturel donné. Ces caractères sont, d'une part, ceux du type biologique et, d'autre part, ceux de l'adaptation des espèces à un mode de vie ou à une niche écologique, plus ou moins spécialisée.

4. Le quatrième volet est un texte court qui apporte, s'il y a lieu, des précisions complémentaires résumant les enseignements que l'on peut dégager des listes et qui achève de caractériser la physionomie de chaque famille en Côte d'Ivoire. Ce texte présente, ensuite, des données originales sur l'utilisation par les ivoiriens de certaines des espèces, soit, par exemple, comme remèdes ou comme aliments: ainsi, dans ce travail j'ai fourni des informations médicinales sur 183 espèces de plantes couramment employées pour le traitement de diverses affections.

5. Le dernier volet concerne les plantes non africaines, volontairement ou involontairement introduites et pouvant présenter un intérêt économique quelconque, en tant que, par exemple, espèces alimentaires, médicinales, ou ornementales.

B. Une liste non commentée de toutes les plantes vasculaires recensées, y compris les ptéridophytes. Il s'agit d'un catalogue complet et de consultation rapide.

C. Une analyse des caractères de la flore ivoirienne, dans le cadre de l'Afrique; cette partie contient, également, les considérations générales pouvant être déduites de cette analyse.

Conclusion

Les résultats de mes investigations peuvent être résumés en cinq points.

1. La flore de la Côte d'Ivoire, à ce jour, comprend 3.660 espèces de plantes vasculaires, réparties en 1.218 genres et 192 familles. Les angiospermes représentent 96% de cette flore, avec 3.517 espèces, 1.158 genres, et 167 familles. Les ptéridophytes ne comptent que 25 familles, 60 genres, et 143 espèces. Cependant, il est possible que la présence de quelques espèces m'ait échappé; mais celles-ci ne sont certainement pas nombreuses et, selon toute vraisemblance, leur omission ne modifie pas, sensiblement, mes évaluations.

2. L'originalité de la flore ivoirienne, dans le contexte afro-tropical, est due à l'existence d'un endémisme relativement important aux niveaux de la famille, du genre et de l'espèce.

3. Le rapport du nombre des espèces au nombre des genres est, dans l'ensemble de la flore ivoirienne, de 3,005. Cette valeur élevée est liée à l'existence de nombreux genres multispécifiques dans certaines familles.

4. Cette étude montre que deux flores, numériquement très semblables, peuvent présenter des différences considérables, liées à un certain nombre de paramètres tels que le nombre des

genres et des familles, la densité de la flore ainsi que le rapport du nombre des espèces au nombre des genres.

5. Enfin, au sein de la flore ivoirienne, j'ai été amené à distinguer deux catégories d'espèces d'inégale importance: *les espèces pluricontinentales,* les moins nombreuses, dont l'aire s'étend, au-delà de l'Afrique, sur d'autres continents; et *les espèces strictement africaines,* qui représentent plus de 82% de la flore ivoirienne.

PLANTES MÉDICINALES: QUELQUES LÉGUMINEUSES UTILISÉES DANS LA MÉDECINE DE TRADITION AFRICAINE EN CÔTE D'IVOIRE

LAURENT AKÉ ASSI[1]

RÉSUMÉ

Afin d'immortaliser et de valoriser la médecine du guérisseur en Côte d'Ivoire, j'ai été amené à entreprendre, depuis 1973, à l'instigation des autorités gouvernementales et scientifiques de mon pays, une vaste enquête à travers tout le territoire, auprès de differentes personnes détentrices des secrets de cette science ancestrale. A la lumière de ces consultations, je dispose d'un nombre considérable de recettes médicamenteuses, dont une infime partie à été publiée sous le titre de "Contribution au recensement des plantes médicinales de Côte d'Ivoire." Ce document de 358 pages, tiré en nombre d'exemplaires très limité, a été distribué à l'occasion du 3ème Symposium Interafricain OUA/CSTR, sur la pharmacopée traditionnelle et les plantes médicinales africaines, tenu à Abidjan, en Côte d'Ivoire, 25–29 Septembre 1979. À ce jour, le reste du document demeure inédit, faute de moyens financiers. Toutefois, en espérant que cette étude sera un jour intégralement publiée, quelques recettes médicamenteuses, concernant certaines légumineuses de Côte d'Ivoire, et se rapportant à deux Mimosacées, sept Caesalpiniacées, sept Papilionacées, ont fait l'objet d'un article particulier que sera communiqué ultérieurement.

ABSTRACT

In order to ensure the survival and show the value of traditional medicine, the governmental and scientific authorities of the Ivory Coast have requested that I undertake a broad study throughout the country. Since 1973 I have interviewed persons in possession of the secrets of this ancient science. As a result of these inquiries I now have a considerable number of medicinal recipes, of which a very few have been published as a "Contribution au recensement des plantes médicinales de Côte d'Ivoire." This 358-page document, printed in very limited quantity, was distributed at the Third Interafrican Symposium of OUA/CSTR font l'objet de l'article qui suit.

En Afrique noire en général, et en Côte d'Ivoire en particulier, en zone rurale surtout, presque chaque habitant connaît et utilise les vertus d'une ou plusieurs espèces végétales. Les guérisseurs ou "tradipraticiens," plus éclairés en la matière que les autres, examinent les malades et posent le diagnostic. Ils récoltent les plantes, préparent et administrent les médicaments. On les rencontre dans tous les milieux, aussi bien dans les villages que dans les villes. En Côte d'Ivoire, par exemple, d'une manière générale, le plus petit hameau possède, au moins, un guérisseur.

Leurs activités thérapeutiques sont habituellement secondaires, car ils sont d'abord agriculteurs, artisans, ou même employés. Ces guérisseurs, hommes ou femmes sont, soit généralistes, soit spécialistes. Ainsi, la médecine de tradition africaine assure de 70–80% de la couverture sanitaire des populations, avec parfois, semble-t-il, plus d'efficacité, et à moindres frais. En effet, les prix de revient des médicaments importés des pays industrialisées sont un frein considérable à leur emploi par la plupart des habitants. Aussi, l'Organisation Mondiale de la Santé a-t-elle émis le voeu de voir se constituer des pharmacopées basées, en priorité, sur les ressources du droguier local.

C'est afin d'immortaliser et de valoriser cette médecine du guérisseur en Côte d'Ivoire que j'ai été amené à entreprendre depuis 1973, à l'instigation des autorités gouvernementales et scientifiques de mon pays, une vaste enquête à travers tout le territoire, auprès de différentes personnes détentrices des secrets de cette science ancestrale.

À la lumière de ces consultations, je dispose d'un nombre considérable de recettes médicamenteuses, dont une infime partie a été publiée sous le titre de "Contribution au recensement des plantes médicinales de Côte d'Ivoire." Ce document de 358 pages, tiré en nombre d'exemplaires très limité, a été distribué à l'occasion du 3ème Symposium Interafricain, OUA/CSTR, sur la Pharmacopée Traditionnelle et les Plantes Médicinales Africaines, tenu à Abidjan, en Côte

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d'Ivoire, 25–29 Septembre 1979. À ce jour, le reste du document demeure inédit, faute de moyens financiers. Toutefois, en espérant que cette étude sera un jour intégralement publiée, je communique, ci-dessous, quelques recettes médicamenteuses, concernant un certain nombre d'espèces de légumineuses de la flore de la Côte d'Ivoire.

Mimosaceae

Dichrostachys cinerea (L.) Wight et Arn. subsp. **africana** Brenan et Brummitt var. **africana**, Greerling, Guide de terrain les ligneux Sahéliens et Soudano-Guinéens: 193. 1982.

Arbuste épineux, atteignant 3 m de hauteur. Feuilles alternes, bipennées, comportant environ 10 paires de pennes; foliolules nombreuses et petites, pubescentes. Inflorescences spiciformes, pendantes, avec fleurs jaunes, hermaphrodites au sommet, et les fleurs neutres, roses ou mauves à la base. Gousses nombreuses, partant du sommet du pédoncule, tortueuses, glabres, brillantes, persistant longtemps sur l'arbre, brunâtres à maturité. Espèce répandue dans toutes les régions de l'Afrique intertropicale, principalement en savane.

Usages. Pour remédier aux palpitations cardiaques, on recommande, aux malades, de boire le d'écocté des racines ou la poudre des racines délayée dans de l'eau. Le décocté des feuilles de la plante, employé pour se laver, a un effet revigorant.

Parkia biglobosa (Jacq.) Benth., Select. Stirp. Am. Hist. 267. 1763. Brenan, Fl. W. Trop. Afr., ed. 2, 1: 487. 1958.

Arbre 8–15 m de hauteur, avec une couronne largement étalée. Feuilles alternes, bipennées, comportant 8–10 paires de pennes; foliolules nombreuses. Inflorescences pendantes, en forme de gourde, comportant un long pédoncule. Fleurs rouges, atteignant 3 cm de long, à anthères noirâtres. Gousses pendantes, atteignant 30 cm de longueur et 2 cm de largeur, jaunes à maturité, puis noirâtres en séchant, contenant des graines ovoïdes entourées d'une pulpe farineuse jaunâtre. Espèce soudano-zambézienne, elle est répandue dans toute l'Afrique de l'ouest. On la trouve aussi aux Antilles où elle a été introduite et cultivée.

Usages. Pour traiter la rougeole, on prescrit, en boisson, aux malades le décocté des écorces de tige. Ce traitement peut être complété par le badigeonnage du corps du malade avec une pâte préparée avec des feuilles fraîche de la plante.

Caesalpiniaceae

Anthonotha crassifolia (Baillon) Léonard, Bull. Jard. Bot. État 25:202. 1955. Keay, Fl. W. Trop. Afr., ed. 2, 1: 473. 1958.

Arbre atteignant 10 m de hauteur, à fût régulier et à cime fortement branchue. Feuilles paripennées, comportant 2–4 paires de folioles opposées; folioles oblongues, 8–20 cm de longueur et 5–9 cm de largeur, vert pâle au-dessus, et gris argenté en dessous, tomenteuses chez les jeunes feuilles. Inflorescences en petites panicules de courts racèmes, très fleuries. Fleurs blanchâtres. Gousses fortes, atteignant 12 cm de longueur et 5 cm de largeur, épaisses, à surface ridée et tomenteuse, couverte de poils bruns. Espèce de forêt dense et de savane, répandue du Mali au Nigeria.

Usages. Pour combattre la fièvre pernicieuse, on recommande, aux malades, de boire et de se laver avec le décocté des feuilles de cette plante et celles de *Bridelia ferruginea* Benth. (Euphorbiaceae) et de *Ximenia americana* L. (Olacaceae).

Cassia sieberiana DC., Prodr. 2: 489. 1825. Keay, Fl. W. Trop. Afr., ed. 2, 1: 425. 1958.

Petit arbre atteignant 10 m de hauteur, à cime étalée et assez dense. Écorce noirâtre. Jeunes rameaux pubescents. Feuilles paripennées, mesurant jusqu'à 30 cm de longueur, comportant 8–16 folioles opposées, elliptiques, oblongues ou ovales, à sommet pointu ou émarginé. Inflorescences en racèmes pendants, mesurant jusqu'à 35 cm de longueur. Fleurs jaunes, atteignant 5 cm de largeur. Gousses cylindriques, indéhiscentes, noirâtres à maturité, mesurant 50–80 cm de longueur, et environ 1,5 cm de largeur. Plante commune dans toutes les savanes de l'Afrique intertropicale. En Côte d'Ivoire, on la trouve à partir des savanes du pays Baoulé.

Usages. La poudre des écorces de racines, mélangée avec de l'eau, constitue une boisson efficace contre l'ictère. La même poudre, mangée telle quelle, est cholagogue. Comme reconstituant, on conseille de se laver avec le décocté des feuilles de la plante.

Daniellia oliveri (Rolfe) Hutch. et Dalz., Kew Bull. 1928: 382. Keay, Fl. W. Trop. Afr., ed. 2, 1: 463. 1958.

Arbre atteignant 15 m de hauteur, à cime obconique et assez dense. Écorce grise, écailleuse. Jeunes rameaux glabres. Feuilles paripennées, mesurant jusqu'à 50 cm de longueur, avec 8–22 folioles ovales, coriaces, glabres, avec des points translucides le long de la marge. Inflorescences en panicules aplaties, mesurant jusqu'à 25 cm de longueur. Fleurs blanchâtres ou verdâtres. Gousses coriaces, aplaties, mesurant 5–10 cm de longueur et 2,5–5 cm de largeur. Plante commune dans toutes les savanes de l'Afrique intertropicale. En Côte d'Ivoire, on la trouve à partir des savanes Baoulé.

Usages. Le décocté des feuilles est prescrit, en boisson, pour remédier aux crises d'appendicite. La même drogue est utilisée pour se laver la tête contre les migraines.

Detarium microcarpum Guill. et Perr., Fl. Seneg. 271, t. 59. 1832. Keay, Fl. W. Trop. Afr., ed. 2, 1: 457. 1958.

Arbuste atteignant 9 m de hauteur, à fût droit, à écorce claire et lisse. Feuilles composées imparipennées, comportant 6–13 folioles alternes, arrondies ou émarginées au sommet, épaisses et coriaces, ovales, avec des points translucides épars, glauques et plus ou moins pubescentes en dessous. Inflorescences en racèmes fasciculés, axillaires, compacts. Boutons floraux densement pubescents. Fleurs jaunâtres. Fruits drupacés, aplatis, fibreux. Espèce soudano-zambézienne, répandue du Sénégal au Cameroun.

Usages. Pour remédier aux douleurs intercostales, on recommande de se laver avec le décocté des feuilles de la plante. Ce traitement peut être complété par le massage de la partie malade avec les marcs résiduels de la décoction. Ce même liquide est conseillée, en boisson, pour calmer les crises de démence. Le traitement peut être complété par des lavements faits avec une solution d'écorces de racines pétries de la plante, que l'on délaye dans de l'eau tiède.

Isoberlinia doka Craib ex Stapf, Kew Bull. Add. Ser. 9: 267. 1911. Keay, Fl. W. Trop. Afr., ed. 2, 1: 468. 1958.

Arbre atteignant 12 m de hauteur. Écorce grise, écailleuse. Rameaux glabrescents. Feuilles atteignant 30 cm de longueur, paripennées, comportant jusqu'à 6 folioles opposées; folioles ovales ou elliptiques, à base asymétrique, arrondie ou cunée. Inflorescences en panicules terminales, atteignant 30 cm de longueur. Fleurs blanches. Gousses oblongues, 15–30 cm de longueur et 5–7 cm de largeur, brunâtres, pubescentes. Plante formant des peuplements denses en région soudano-zambézienne. On la trouve de la Guinée au Soudan.

Usages. Pour traiter l'hydrocéphalie, on conseille de donner à boire et de laver les malades avec le décocté des feuilles de cette plante, mêlées avec celles de *Pseudarthria fagifolia* Baker (Papilionaceae) et de *Ximenia americana* L. (Olacaceae).

Swartzia madagascariensis Desv., Ann. Sci. Nat. (Paris), 9: 424. 1826. Keay, Fl. W. Trop. Afr., ed. 2, 1: 446. 1958.

Arbuste atteignant 5 m de hauteur, à écorce lisse, se desquamant en écailles minces. Rameaux pubescents. Feuilles imparipennées, mesurant jusqu'à 20 cm de longueur, comportant 5–15 folioles opposées ou alternes, ovales ou elliptiques, pubescentes ferrugineuses. Inflorescences en racèmes axillaires ou quelquefois des fleurs solitaires. Fleurs pubescentes, ayant un seul pétale blanc mesurant environ 2,5 cm de longueur. Gousses cylindriques irrégulières, atteignant 30 cm de longueur et 2 cm de diamètre, brun noir, luisantes. Espèce soudano-zambézienne, elle est répandue dans toute l'Afrique intertropicale. On la trouve à Madagascar ainsi que dans les îles Mascareignes.

Usages. Le décocté des racines est prescrit, en boisson, pour remédier aux divers maux de ventre accompagnés de vomissements. Pour le même effet, on recommande aux malades de se laver avec le décocté des feuilles de la plante.

Tamarindus indica L., Sp. Pl., ed. 1: 34. 1753. Keay, Fl. W. Trop. Afr., ed. 2, 1: 477. 1958.

Arbre atteignant 10 m de hauteur, à cime dense. Rameaux légèrement pubescents. Feuilles paripennées, mesurant jusqu'à 15 cm de longueur, comportant 20–30 folioles opposées, étroitement oblongues, à sommet arrondi ou émarginé, à base arrondie ou asymétrique, glabrescentes. Inflorescences terminales, en racèmes ou en panicules, atteignant 15 cm de longueur. Fleurs me-

surant environ 2,5 cm de largeur, jaunâtres, veinées de brun. Gousses indéhiscentes, cylindriques, plus ou moins toruleuses, atteignant 15 cm de longueur, et jusqu'à 2,5 cm de diamètre, brunâtres. Espèce très répandue dans les régions sèches de l'Afrique intertropicale. On la trouve à Madagascar et en Amérique tropicale. Elle est souvent cultivée.

Usages. Le décocté des feuilles constitue une boisson laxative. Le même décocté, employé pour se laver, est un revigorant efficace.

Papilionaceae

Abrus precatorius L., Sp. Pl., ed. 12: 472. 1766. Hepper, Fl. W. Trop. Afr., ed. 2, 1: 574. 1958.

Liane grêle, volubile, glabre. Feuilles alternes, paripennées, comportant 7–10 paires de folioles oblongues. Inflorescences en grappes axillaires. Fleurs blanchâtres ou roses. Gousses petites, trapues, contenant 5–6 graines ovoïdes, rouge vif, avec une tache noire à la base. C'est une espèce de formations secondaires des régions forestières, dont l'aire se prolonge en savane. On la trouve dans toute l'Afrique intertropicale ainsi que dans les autres parties tropicales du monde.

Usages. Comme aphrodisiaque, on conseille de manger les feuilles fraîches de la plante, avec des bulbes de *Cyperus esculentus* L. (Cyperaceae). Pour remédier aux menaces d'avortement et aux accouchements prématurés, on recommande, en lavement, une solution faite avec des feuilles fraîches pétries de la plante, que l'on délaye dans de l'eau tiède.

Afrormosia laxiflora (Benth. ex Baker) Harms, Notizbl. 21, 2: 64. 1911. Hepper, Fl. W. Trop. Afr., ed. 2, 1: 510. 1958. = **Pericopsis laxiflora** (Benth. ex Baker) Van Meeuwen.

Arbre 5–10 m de hauteur, à tronc tortueux, à écorce assez lisse, brunâtre. Jeunes rameaux pubescents. Feuilles imparipennées, 15–35 cm de longueur, comportant 9–13 folioles alternes, ovales ou elliptiques, glabrescentes ou glabres. Inflorescences ou racèmes ou en panicules, atteignant 15 cm de longueur. Fleurs blanchâtres, mesurant environ 1 cm de longueur. Gousses elliptiques, atteignant 10 cm de longueur et 2–3 cm de largeur, aplaties, glabres. Espèce répandue dans toute l'Afrique intertropicale, dans les régions soudano-zambéziennes.

Usages. Pour remédier au palpitations cardiaques, on préconise l'ingurgitation d'une solution faite avec les jeunes feuilles pétries de la plante, que l'on délaye dans de l'eau. Pour le traitement des mêmes maux, ces feuilles peuvent être mangées telles quelles. Pour soigner les douleurs lombaires, on conseille de faire des applications locales avec une pâte obtenue à partir des écorces de tige de la plante.

Eriosema glomeratum (Guill. et Perrier) Hook. f., Fl. Nigr. 313. 1849. Baker, Fl. Trop. Afr. 2: 228. 1871. Hepper, Fl. W. Trop. Afr., ed. 2, 1: 558. 1958.

Sous-arbrisseau atteignant 2 m de hauteur, très branchu, à rameaux pubescents. Feuilles trifoliolées; folioles lancéolées, mesurant jusqu'à 12 cm de longueur et 2 cm de largeur, pubescentes. Inflorescences en glomérules axillaires, courtement pédonculées. Fleurs jaunes, à lobes du calice filiformes, longuement poilus. Gousses à surface ondulée, 1–1,2 cm de longueur et 7–8 mm de largeur, hirsutes, contenant 1–2 graines. Plante répandue dans toutes les savanes de l'Afrique intertropicale.

Usage. Le décocté des feuilles est prescrit, en boisson, contre les migraines.

Eriosema griseum Baker, Fl. Trop. Afr. 2: 228. 1871. Fl. Congo Belg. 6: 224. 1954. Hepper, Fl. W. Trop. Afr., ed. 2, 1: 558. 1958.

Sous-arbrisseau atteignant 40 cm de hauteur, ramifié dès la base à partir d'une souche ligneuse. Feuilles trifoliolées; folioles oblancéolées, arrondies à largement émarginées au sommet, 2,5–5 cm de longueur et 1–2,5 cm de largeur, couvertes de poils blanc duveteux. Inflorescences capituliformes, subsessiles, subterminales, atteignant 4 cm de longueur et 3 cm de diamètre. Fleurs dressées, jaunes, à corolle généralement masquée par le calice assez développé. Gousses poilues, atteignant 1 cm de longueur. Espèce de savane, poussant dans les endroits dégradés.

Usage. Comme aphrodisiaque, on recommande de mâcher et d'ingurgiter l'extrait des racines de la plante.

Pterocarpus erinaceus Poiret, Encycl.: 419. 1804. Hepper, Fl. W. Trop. Afr., ed. 2, 1: 518. 1958.

Arbre 8–10 m de hauteur, écorce écailleuse, dure, noirâtre. Rameaux glabrescents. Feuilles imparipennées, comportant 4–5 paires de fo-

lioles alternes ou subopposées, elliptiques, courtement pubescentes sur la face inférieure. Inflorescences en panicules, 10–20 cm de longueur. Fleurs jaunes, atteignant 1,5 cm de longueur. Gousses ailées, suborbiculaires, garnies de nombreuses soies rigides et épineuses au centre. Plante soudano-zambézienne, répandue dans toute l'Afrique de l'ouet.

Usages. Le décocté des feuilles est precrit, en boisson, pour remédier aux accouchements prématurés et aux menaces d'avortement. Ce décocté, en bain de vapeur du sexe, a un effet aphrodisiaque. Le décocté des écorces de tige de la plante est recommandé, en boisson, contre la dysenterie.

Rhynchosia minima (L.) DC. var. **minima**, Prodr. 2: 385. 1825. Baker, Fl. Trop. Afr. 2: 219. 1871. Berhaut, Flore Illustrée du Sénégal, tome 5: 491. 1976.

Plante herbacée, volubile, à tiges grêles. Feuilles alternes, trifoliolées; folioles ovales triangulaires, 2–4 cm de longueur et 1,5–3 cm de largeur, à base cunée ou arrondie, à sommet obtus. Inflorescences en racèmes axillaires lâches, atteignant 12 cm de longueur. Fleurs jaunes, atteignant 1 cm de longueur, à étendard veiné de rouge. Gousses 1,5–2 cm de longueur, contenant 2 graines. Espèce pantropicale, on la trouve dans les savanes en Côte d'Ivoire.

Usage. Pour hâter leurs premiers pas, il est recommandé de donner à boire aux bébés et de les laver avec le décocté des feuilles de la plante.

Uraria picta (Jacq.) DC., Prodr. 2: 324. 1825. Hepper, Fl. W. Trop. Afr., ed. 2, 1: 587. 1958.

Plante herbacée, plus ou moins ligneuse à la base, atteignant jusqu'à 60 cm de hauteur, à tige pubescente. Feuilles imparipennées, comportant 2–4 paires de folioles opposées; folioles longueument oblongues lancéolées, 10–15 cm de longueur et 1–2 cm de largeur, à base arrondie, à sommet graduellement retréci, scabres sur les 2 faces; stipules triangulaires, atteignant 1 cm de longueur. Inflorescences spiciformes terminales, atteignant 15–35 cm de longueur. Fleurs nombreuses, denses, à corolle bleu mauve, mesurant 1 cm de longueur. Gousses courtes, tordues en acordéon, composées de 4–5 articles. Espèce de savane, elle est répandue dans toute l'Afrique intertropicale. On la trouve en Australie.

Usages. Le décocté des racines est prescrit, en boisson, contre la toux. Le décocté des feuilles est une boisson efficace contre le rhumatisme articulaire. Contre la migraine, il est recommandé de priser la poudre des feuilles séchées de la plante. Afin de hâteur leurs premiers pas, on conseille le badigeonnage de la poitrine des bébées avec une pâte obtenue à partir des graines de la plante.

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SESAMUM INDICUM L. (PEDALIACEAE): ETHNOBOTANY IN SUDAN, CROP DIVERSITY, LIGNANS, ORIGIN, AND RELATED TAXA[1]

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ABSTRACT

Sesame is the most important oil crop grown in Sudan and, aside from cotton, is the primary cash crop and major source of currency. Sudan produces 40% of the sesame in world trade, as well as most of the seeds for manufacturing *halva* (*tahneeya* in Sudan)[3] in Egypt (Hassan Daoud, Saad Sweets, Khartoum, pers. comm.). The oil is highly regarded for its resistance to oxidation and rancidity, even when stored at ambient air temperatures. The presence of sesamin and sesamolin, natural antioxidants found uniquely in sesame among vegetable oils, is responsible for this property.

RÉSUMÉ

Le Sésame est la principale espèce oléifère du Soudan; c'est la deuxième plante d'importance économique après le Coton et une source précieuse de devises. Le Soudan produit 40% de la production mondiale de Sésame, ainsi que la majorité des graines utilisées pour la fabrication du *halva* (*tahneeya* au Soudan) produit en Egypte. L'huile de Sésame est très appréciée car, même lorsqu'elle est stockée à temperature ambiante, elle résiste bien à l'oxydation et au rancissement. Cette propriété est due à la présence de sésamine et de sésamoline, des antioxydants naturels qui n'existent dans aucune autre huile végétale.

BOTANICAL FEATURES AND DIVERSITY OF SESAME IN SUDAN

Cultivars of sesame (*Sesamum indicum* L.) differ considerably from each other in their branching habit, flower color, in the size, shape and arrangement of capsules, and in the color and size of seed. There may be 1–3 capsules per axil, and one or more axils per node. The capsules may be 2–4 carpellate. A single character occasionally may also vary on the same plant or even on the same branch. This is true of shape of leaves, position of flowers, number of fruits per axil, and number of carpels per capsule. In general the cultivated plant can be distinguished from other species of *Sesamum* by its palmately compound leaves, hairy white or pale lavendar corolla, thin-walled, dehiscent capsules, and smooth seed faces. Seeds range in color from white to black with intermediate colors of beige, tan, red, brown, and gray.

There is a remarkably high level of morphological variation within cultivated sesame in the Nuba Mountains of Sudan (Yassin, 1978; Bedigian & Harlan, 1983). Compared with the rest of the Sudan, where relatively few distinct varieties occur, the Nuba Mountains is a small region with dozens of sesame landraces. The area may realistically be called a microcenter (Harlan, 1951). The Nuba people are geographically isolated and culturally diverse in religion, language, material inventory, and agricultural practices. This contributes to the diversity in their culti-

[1] Much of this report is based on field research carried out in the Sudan between October 1979 and January 1980. The Sudanese government limits access to some of the areas but special permission was received to travel there. Appreciation is extended to the Crop Evolution Laboratory, Department of Agronomy, University of Illinois; officials of the Ministry of Interior of the Democratic Republic of the Sudan; officials at the Agricultural Research Corporation and the Nuba Mountains Corporation in Kadugli; Roger Billington of Hunting Technical Services and his Sudanese counterpart, Ahmed Khalid Showk; Mahmoud A. Mahmoud, then at the Agricultural Research Corporation, Wad Medani; Yvette Scheven, Africana bibliographer, and the superb library and interlibrary loan service of the University of Illinois; and to the people of the Nuba Mountains. This work was supported in part by the University of Illinois NSF Regional Instrumentation Facility, grant no. NSF CHE 79-16100. We thank the administrative curator of the Missouri Botanical Garden herbarium for permission to remove seed material for this analysis.

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[3] Most vernacular names in the text are in the Arabic language and are commonly used by Nuba and Arab alike.

vars. However, many races also occur within a single habitat.

The Nuba themselves identify specific cultivars of sesame with specific Nuba people and their inselberg hills (called *jebels* in Arabic) and are aware of their particular oil content, seed color, and resistance to locust attack or disease. A variety of sesame with large gray seeds (*morawi*) originated in the Moro Hills. It is a successful cultivar grown today by Nuba outside the Moro *jebels* but retaining the name of the region where it originated. One of the most popular landraces grown in Tukswana and Dubeibat, 35 km NE of Kadugli, is *abu sindook,* "one distinguished by a trunk," suggesting its shape, multicarpellate condition, and abundant seeds. *Dinderawi* has gray seeds and capsules that are 50% longer than any others observed. The Dinder Game Reserve contains a large population of giraffes. Dinder is not an Arabic word. The name of this long-capsuled cultivar suggests a giraffe's height.

The Nuba have developed cultivars and special techniques appropriate to each ecological situation. Early maturing crops are chosen for terraced land, or light, stabilized, sandy, *qoz* soils where water is scarce. These crops include sesame, pearl millet (*Pennisetum americanum* (L.) Leeke), and roselle (*Hibiscus sabdariffa* L.), which provides the national drink of the Sudan (*karkadeh*). It is frequently intercropped with an early-maturing *khafif* sesame cultivar named *hirehir* that matures in 70 days. In contrast, on the heavy clay soils with abundant water reserves, late-maturing *tegil* "heavy" types of sesame require up to 180 days to mature. Seeds from sesame varieties growing on the *qoz* and on the clay plains range in color from white to black.

Selection of sesame cultivars according to their specific oil content or flavor is common. The distinctive red-seeded sesame of Kordofan is a unique form with high oil content found exclusively in the Sudan. It is grown primarily in the Nuba Mountains and to a lesser extent in the sesame-growing region around Gedaref, but growers there say that their seeds originated outside the area. At the sesame auction in the main market depot of El Obeid, all red-seeded sesame varieties are called *jebeli,* suggesting their origin in the Nuba Mountains. Kordofan Red is a tall, profusely branched, robust type with many large capsules and brick red seeds containing up to 60% oil, cultivated by farmers who raise them as an oil seed. They seem to be particularly well adapted to the Nuba Mountains and can withstand high winds, heavy rains, and the bacterial leaf spot or "blood" disease (*Xanthomonas sesami* Sabet & Dowson and *Pseudomonas sesami* Malkoff). One local name for the red-seeded variety is *denemet,* meaning dynamite, possibly referring to its high oil content or the crackling sounds of dehiscing sesame capsules. Growers and middlemen, however, say the red-seeded type is bitter and hard to digest. Varieties with white seeds are "sweet" and are preferred in confectionary preparations.

At Tebeldiko, near Lagowa in the western *jebels,* Daju Nuba cultivate red and white varieties separately in adjacent fields. They understand that each variety will breed true. The two varieties have different heights, branching habits and other characteristics, so the Daju Nuba thin these varieties to different densities. Fields of the red-seeded variety mature earlier and are harvested in October, while adjacent fields of the white-seeded variety are still green. Red-seeded plants are 1.5–2 m tall, robust, profusely branched, with bicarpellate capsules ca. 1 cm wide and 3–4 cm long and with rugose seed coats. In contrast, plants with white seeds are ca. 1–1.2 m tall, less branched, with bicarpellate capsules ca. 2–3 cm long, and with smooth seed coats.

Nuba Ethnobotany

The Nuba use sesame and its oil daily as food, medicine, cosmetics, and gifts of exchange for many rituals (Bedigian & Harlan, 1983).

Nuba householders extract oil from sesame seeds by pounding them in a wooden mortar and pestle (*funduk*). The resulting coarse paste is transferred to a stone, clay, or gourd slab and kneaded into a soft paste that is placed in a square metal can. Boiling water is poured over the paste and the oil is skimmed off after it rises to the surface.

A sauce often eaten with sorghum bread is prepared by mixing sesame seed paste with water, salt, red pepper (*Capsicum annuum* L.), and onions, if available (*Allium cepa* L.). A refreshing salad consists of chopped cucumber (*Cucumis* sp.), onion, and toasted sesame seeds. A filtrate of the ashes of burnt sesame stalks is added to stews because it is considered to have nutritional value, containing many minerals. The filtrate is also used to tenderize dried okra [*Abelmoschus esculentus* (L.) Moench] or *moluchia* (*Corchorus olitorius* L.) by breaking down the cellular struc-

ture. Crushed sesame seeds mixed with sugar or honey constitute a favorite dessert. If sugar or honey is not available, salt is added to roasted sesame seeds for a snack.

Sesame oil is used cosmetically by Nuba as a body massage that makes the skin shine and as a hair dressing, alone or mixed with red ochre. It is used medicinally to heal earaches. The oil of red-seeded sesame is recommended for many illnesses. A mixture of sesame seeds cooked with cowpeas and wild okra is recommended to relieve constipation and upset stomach.

The Nyima Nuba in the northern village of Kelara are heavily influenced by Islam; there, sorghum is strictly a man's crop whereas sesame is a woman's crop. This may be left over from the time of Arab raids when protection of women was essential and they were restricted to their homesteads. It may also reflect the Islamic custom of segregation of women. As a consequence, men cultivate sorghum on the far farms. Their sole contribution to the sesame plot, near the homestead, is to clear the land and construct an enclosure (*zereeba*), usually of thorn branches, to exclude browsing animals. Thereafter women alone broadcast the seed, hoe weeds, and harvest the crop. Men do not set foot inside the sesame nursery after it is planted.

Sesame Lore from Other Parts of Sudan

Everywhere in the Sudan, a crunchy sesame candy called *halawa moolid simsimiya* is prepared with sesame seeds and carmelized sugar to commemorate the *moolid*, or birthday, of the prophet Muhammad.

Sesame oil is used as a skin emollient, a necessity in the hot, dry climate of Sudan. It is also used as a fixative of henna, the red-brown dye derived from *Lawsonia alba* Lam. Celebrations such as weddings, childbirths, etc. include a party, *al henna*, for applying the decorative designs on nails, hands, and feet.

The sesame plant and its seeds are associated with special powers. Folklore and popular usage reflect these qualities. Sesame capsules open with such explosiveness upon drying that when one stands in a sesame field at harvest time, one hears snapping, crackling, and popping sounds. A red-seeded cultivar grown in the Sudan might have acquired its popular name *denemet*, or dynamite, from this phenomenon (Bedigian & Harlan, 1983). The tale of Ali Baba and the Forty Thieves from the *Thousand and One Arabian Nights* incorporates the powerful shattering of sesame capsules in the magical incantation "Open, Sesame" to open treasures.

The popular Sudanese love song, *Simsim al Gedaref*, is named after the tiny size, but significant value, of sesame seeds. The words describe the beloved as a small but precious girl:

> Oh *simsim al Gedaref*,
> still young, she doesn't know (about love),
> (Speaking to his heart)
> I'm always trying to teach you the right way
> but you won't follow
> You insist on loving her.

Gedaref is the largest sesame-growing area in the Sudan. *Simsim* is a woman's pet name.

One of the *jebels* south of Gedaref is called Jebel Simsim. Local informants said that the *Anaj* (kings during the Fung dynasty) named the jebels in honor of favorite daughters to immortalize them. The names of these jebels go back at least 500 years.

Sesame oil is extracted in quantity at a workshop called an *asara*. A blindfolded camel is harnessed to a wooden mortar and pestle made of the durable wood of *Acacia nilotica* (L.) Willd. ex Delile. As the camel walks in a circle, the seeds are ground, releasing the oil. After the oil is expressed, the protein-rich residue makes an excellent livestock feed. The high oil content of sesame seeds (45–63%) inspired a Sudanese proverb: "Just like sesame, if you don't press it, it won't give oil."

Near Wild Relatives in Sudan

Sesamum latifolium Gillett (*Thomas 3708*, K) is widespread in Sudan (Bedigian, pers. obs.) and grows in disturbed and undisturbed habitats. It invades abandoned agricultural fields but also occurs in undisturbed gravelly soil near boulder outcrops. Nuba call it *simsim al culb* ("dog's sesame") or *simsim al marfayeen* ("wolf's sesame"), and they were bewildered that I collected its seeds, which they regarded as useless and a nuisance. It often grows at the rocky bases of jebels in association with the *tebeldi* tree, *Adansonia digitata* L., the woody herb *Leonotis africana* (Beauv.) Briq., and *Rogeria adenophylla* Gay ex Delile, another species of Pedaliaceae. This *Rogeria* species is called *simsim al afrit* ("devil's sesame") because its woody capsules have long, spikelike thorns and its seeds are totally unpalatable.

TABLE 1. Lignan content of seeds of species of *Sesamum*.

	Seed	Sesamin	Sesamolin
Sesamum alatum Thonn.	f	–	–
S. angolense Welw.	h	+	+
S. angustifolium (Oliver) Engl.	f	+	+
S. calycinum Welw.	h	+	+
S. capense Burm.	h	–	trace
S. indicum L.	f	+	+
S. latifolium J. B. Gillett	f	+	–
S. orientale var. *malabaricum* Naray.	f	+	+
S. pedaloides Welw. ex Hiern	h	trace	–
S. radiatum Schum. & Thonn.	f	+	–
S. rigidum Peyr. ssp. *merenskyanum* Ihlef. & Seidenst.	h	–	–
S. triphyllum Welw. ex Asch.	h	–	–
Univ. of Illinois #7308: weedy escape from Australia	f	+	+

f = fresh seed; h = herbarium specimen.

Sesamum latifolium is a robust annual with a woody, many-branched stem, more or less cordate leaves with serrate to crenate margins, and a white corolla with several fine purplish-red lines on the lower lip and pink shading deep inside the corolla. It flowers continually from July to December. There is generally one flower per axil and often three axils per node. At each side of the corolla are extrafloral glands, which are black when immature and yellow when mature. The woody capsule has acute lobes at its base, is indehiscent, and sets black, radially reticulate seed that are dormant for several years.

Despite the fact that it was collected in 1837–1838 by Kotschy during his travels in Sudan, *Sesamum latifolium* was validly described as a species only in 1953 by Gillett. It was omitted from the flora of Sudan published thereafter (Andrews, 1956). Consequently *S. latifolium* from Sudan is often misidentified as *Sesamum radiatum* Schumach. Neither Gillett (pers. comm., 1980, 1984) nor Ihlenfeldt & Grabow-Seidensticker (1979) were aware that *Sesamum latifolium* occurs in Sudan. Gillett's (1953) concern that Kotschy's collection was "placed in this species with some doubt" is unnecessary. In fact Kotschy's collection (*Kotschy 320*) is the earliest known specimen of the species.

Sesamum latifolium is adapted to heavy clay soils and appears to be immune to the bacterial leaf-spot disease. Sudanese breeders have been unsuccessful in transferring these traits to cultivated sesame by interspecific hybridization, and our attempts in the Crop Evolution Laboratory also were unsuccessful, yielding only a few sterile seeds.

The species occurs throughout central Sudan. It grows at Agadi, on fallow agricultural lands between the two Niles; at Buram and Talodi, villages in the southern Nuba Mountains, in Kordofan Province; and abundantly in eastern Sudan, near Gedaref and south along the chains of mountains near Doka and Jebel Semasim. Especially in these eastern jebels, it is a pioneer species, like *Rogeria adenophylla,* and capable of degrading the rock where it grows.

In contrast, another wild species, *Sesamum alatum* Thonn. (*Kotschy 106,* K), grows on the sandy *qoz* soils and is a frequent weed in cultivated sesame fields or areas of abandoned cultivation. Its corolla is pink to red and radially symmetrical, unlike the bilaterally symmetrical corolla of cultivated sesame. Its capsule is slender and graceful and tapers at the tip, suggesting its local name *simsim al ghazal* ("gazelle's sesame"). Another local name, *simsim al jumal* ("camel's sesame"), might be related to the environment in which this species occurs. It is grazed by camels on *qoz* soils. Its black seeds are muricate with a paper-thin, broad wing at each end.

LIGNANS AND ORIGIN OF THE CROP

Although the use of chemical data to establish phylogenetic relationships is important, lignans have not been widely used for these analyses. Lignans are widespread in the plant kingdom (Hearon & MacGregor, 1955; Robinson, 1980), occurring in heartwood, leaves, and resinous exudates of plant families as distantly related as the Gingkoaceae and the Asteraceae. Approxi-

TABLE 2. Lignan content of seeds of related genera of *Sesamum*.

	Seed	Sesamin	Sesamolin
Ceratotheca sesamoides Endl.	f	+	trace
C. triloba Meyer ex Bernh.	h	trace	–
Holubia saccata Oliver	h	trace	–
Pedalium murex L.	h	trace	–
Pretrea zanguebaricum Gay	h	trace	–
Pterodiscus aurantiacus Welw.	h	–	–
Rogeria adenophylla Gay ex Delile	f	–	–
Sesamothamnus busseanus Engl.	h	+	+

f = fresh seed; h = herbarium specimen.

mately three dozen compounds are known at present (Robinson, 1980). Relationships of members of several families, including the Asteraceae (Hänsel et al., 1964; Greger, 1979, 1981), have been studied with lignans, but these compounds have not been used to study the phylogeny of plant families related to Pedaliaceae.

The families considered to be the nearest relatives of the Pedaliaceae—Bignoniaceae and Acanthaceae—also contain lignans. Sesamin and another lignan, paulownin, have been isolated from the wood of *Paulownia tomentosa* Steud. (Bignoniaceae) (Takahashi et al., 1963; Takahashi & Nakagawa, 1966). NMR spectral analysis of the stereochemistry of the latter compound shows structural similarity to sesamin and sesamolin. Roots and stems of *Phyllarthron comorense* and *Tabebuia rosea* (Bignoniaceae) yielded sesamin and paulownin, respectively (Joshi et al., 1976). Sesamin, asarinin, sesamolin, and a new compound, simplexolin, were isolated from *Justicia simplex* (Acanthaceae) (Ghosal et al., 1979).

Two lignans, sesamin and sesamolin, occur in sesame oil. These compounds are antioxidants and powerful insecticidal synergists. Cultivars of sesame were screened to determine how widely lignans occur (Bedigian et al., 1985). All lines tested contained sesamin and sesamolin. Their occurrence in other species of *Sesamum* and other genera of Pedaliaceae varied.

The wild progenitor of sesame has not been established with certainty, and the literature asserts with equal frequency that the center of origin of the crop is in Africa and Asia. A recent proposal that *Sesamum latifolium* is the progenitor of sesame and that the crop originated in Africa was accompanied by a division of the genus *Sesamum* into four sections (Ihlenfeldt & Grabow-Seidensticker, 1979). The chromosome number of *S. latifolium* is reported to be $2n = 32$ (Ihlenfeldt & Grabow-Seidensticker, 1979).

We examined near relatives of cultivated sesame to see how widespread these lignans are in the genus *Sesamum* (Table 1). Seeds of *S. latifolium* consistently lack sesamolin (Bedigian et al., 1985). Reciprocal crosses between the crop and *S. latifolium* have been attempted without success.

The nearest wild relative of cultivated sesame is the taxon from India known as the wild gingelly of Malabar, named *Sesamum orientale* var. *malabaricum* Naray. in the original description (1950). It occurs wild in the Walayar Forest, Palghat District, Kerala (*Joseph 33062,* MH; Bedigian, pers. obs.), and in the Ichipalli Forest Reserve, Coimbatore (*Narayanaswamy 7818g,* MH). This is the probable ancestor of the crop (Bedigian et al., 1985). Its chromosome number is reported to be $2n = 26$ (John et al., 1950), the same as the crop. Like cultivated sesame, it contains both sesamin and sesamolin. Numerical analyses confirm the similarity between this wild Indian variety and the crop (Bedigian et al., 1986). Reciprocal crosses with the crop were fully fertile using var. *malabaricum* as both male and female parent.

Sesamin and sesamolin were also found in seed oils of *Sesamum angolense, S. angustifolium, S. calycinum,* and a weedy escape from Australia. Oils of *S. latifolium* and *S. radiatum* contained sesamin but not sesamolin. The presence of lignans in other species was more difficult to establish. These compounds were absent from fresh seed of *Sesamum alatum.* Even when 10 g of seed of *S. alatum* was extracted as described (Bedigian et al., 1985), the sample contained only nonlignan lipids as indicated by NMR spectral analysis. TLC also confirmed that lignans were absent. The absence of lignans from both *S. ala-*

TABLE 3. Voucher numbers of herbarium specimens studied.

Taxon	MO Number	Date	Country
Sesamum angolense	2652241	20 Aug. 1976	Malawi
S. calycinum	2947307	22 Feb. 1979	Malawi
S. capense	2341123	1974	Mozambique
S. pedaloides	2429666	5 Nov. 1976	S.-W. Africa
S. rigidum ssp. *merenskyanum*	2614251	2 Apr. 1977	South Africa
Ceratotheca triloba	2832733	1 Jan. 1979	Mozambique
C. triloba	2186743	22 Dec. 1971	South Africa
C. triloba	2449087	9 Mar. 1977	Swaziland
Holubia saccata	1602340	1948	Rhodesia
Pedalium murex	2829866	30 May 1976	Ghana
Pretrea zanguebaricum	2448044	14 Apr. 1973	Botwsana
Pterodiscus aurantiacus	2404153	3 Sept. 1975	South Africa
Sesamothamnus busseanus	2892717	Nov. 1970	Kenya

tum and *S. capense* is noteworthy, as both are species with winged seeds in the section Sesamopteris, which is relatively isolated within the genus.

Observation of the absence of sesamolin from *S. radiatum* was used to correct the identification of an unusual morphotype in the sesame germplasm collection from Sudan that also lacked sesamolin. The germplasm collection maintained by the Agricultural Research Corporation, Kadugli, Sudan, contains line 144 that was identified as *Sesamum indicum*. The shape and color of the corolla, the overall plant habit, and the fact that this cultivar remained green well after all other lines in the nursery had begun to senesce suggested that it differed greatly from other cultivars of sesame. It was the last line to be harvested. Testa ornamentation on seeds from line 144 appeared similar to those of specimens of *Sesamum radiatum* (Bedigian, unpubl. data). Extracts of both samples were compared by TLC. The chromatograms were identical, suggesting that it is probable that line 144 is actually *S. radiatum*.

In this study, seeds of *Sesamum angolense* from herbarium specimens showed the presence of both sesamin and sesamolin. A spot identical in Rf to sesamin was observed, confirming the report of Pearman et al. (1951). We cannot exclude the possibility, however, that the compound is sesangolin (Jones et al., 1962), not sesamin. Confirmation with fresh seed material and NMR spectroscopy could remove this problem.

Other genera of Pedaliaceae vary considerably in their content of lignans (Table 2).

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THE SUMA AND THEIR SORGHUM: ETHNOLOGY AND ECONOMICS[1]

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ABSTRACT

Sorghum, or guinea corn, provided the staple food for most of the inhabitants of the savanna in the Central African Republic (CAR) until the 19th century, when manioc began to replace it. Sorghum grain was used to make staple flour, but other parts of the plant were also employed for a large number of secondary uses. By the time the French gained effective control of the territory in the first decades of the 20th century, most peoples of the large Gbaya family (including the Suma) of the western CAR (and eastern Cameroon) had already adopted manioc as their staple. Sorghum was still being cultivated by many Gbaya peoples primarily because it was used to brew beer and other beverages, and thus the secondary uses of the plant have been retained and are common today.

RÉSUMÉ

Le sorgho ou blé de Guinée ('guinea corn') était la nourriture de base pour la plupart des habitants de la savanne en République Centre Africaine (RCA) jusqu'au 19ème siècle quand elle commençât à être remplacée par le manioc. Les graines de sorgho étaient utilisées pour faire la farine de base, mais d'autres parties de la plante servaient aussi pour de multiples usages moins importants. Au moment où les français avaient acquis le contrôle du territoire au début du 20ème siècle, la plupart des peuples de la grande famille des Gbaya (qui comprend les Sumas) dans la partie occidentale de la RCA (et l'est du Cameroun) avaient déjà adopté le manioc comme aliment principal. Le sorgho continuait d'être cultivé par de nombreux peuples Gbaya principalement parce qu'il était utilisé pour fair de la bière et d'autres boissons et, donc, les utilisations accessoires de la plante ont été conservées et sont pratique courante aujourd'hui.

THE SUMA PEOPLE

The "Snake-Bite-You" Suma, as they distinguish themselves, are among the northernmost representatives of the Gbaya peoples who speak Adamawa-Ubangian languages belonging to the Nile–Congo family. No monographs or publications of any kind regarding the Suma are available, but they are classified linguistically with the Gbeya. The Suma language uses three distinct tone levels, however, while Gbeya uses only two. In most other ways their language and culture are very similar (Samarin, 1966; Bradshaw & Sankpam, in prep.; Bradshaw, unpubl.).

Harlan & Stemler (1976) claim that there is a "crude correspondence between the distribution of the basic races of sorghum and the distribution of the major language groups." The Guinea type is said to be associated with the Niger–Congo family, and *Sorghum guineense* Stapf is in fact the predominant type among the Gbeya. The Suma's Chari–Nile language-speaking neighbors to their immediate north, the Sara people, apparently use mostly Caudatum-type sorghum. The Sara have not adopted manioc as their staple, so the Suma live on the border between users of different sorghums and different staples.

Suma territory lies at the coordinates of roughly 7°N, 17°E in a "Sudano-Guinean" phytogeographic zone (cf. Boulvert, 1980; Motte, 1980). It is characterized as clear woodland savanna of phyrophilic species. The altitude of the prefecture varies between 500 and 1,000 m, the average annual rainfall is 1,320 mm, and the dry season lasts about five months (Sillans, 1958).

MAJOR USES OF THE SORGHUM PLANT: AN OVERVIEW

The average Suma villager knows thousands of uses for plants and can identify hundreds of species without difficulty, but no plant is used so thoroughly and ingeniously as sorghum. Although the list of uses presented here may appear fairly comprehensive, it in fact represents only an initial list offered by an urban-dwelling Suma

[1] Research was carried out during six years of residence in the Central African Republic as a public health administrator. Identification of all the plants cited is by botanist J. Michael Fay. The basic list of uses was kindly provided by Isaac Kparekuti. Discussions with Joel Nangbei were most helpful.

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TABLE 1. Major uses of the sorghum plant by the Suma (Kparekuti, unpubl.).

Uses of the grain:	
1. de ne biribiri	= make sorghum beer
2. de ne harge	= make hard liquor
3. de ne sara	= make a sorghum-based drink
4. de ne lo'boto	= make a sorghum-based drink
5. de ne samsam	= make a sorghum-based drink
6. de ne kafee	= make a coffee substitute
7. de ne defa harge	= make a starter for liquor
8. de ne mo yong yok	= use as trap bait
9. de ne kuru fon	= mix with beans for a snack
10. de ne fum	= make into flour (#11–16 below)
Uses of the flour:	
11. ru ne kam	= stir into *kam*, or staple dough
12. wun ne ko	= mix in water to make porridge
13. de ne makala	= make *makala* bread balls
14. de ne bo'du	= make a drink called *bo'du*
15. de ne kulu	= make a drink called *kulu*
16. fo'di ne wofi	= mix with gluant in sauces
Uses of the stalk:	
17. de ne guro	= make *guro* stand platform
18. de ne kandara	= make *kandara* stand platform
19. de ne kpangba dam	= make *dam* grain storage platform
20. de ne pal tende	= make *pal* cotton stand platform
21. de ne yawa sunu	= make sesame harvest platform
22. de ne pamba fon	= make sorghum storage stand platform
23. de ne mbale kora	= make light goat pen fence
24. de ne ndela yok	= make *yok* hunting net supports
25. de ne sak gburka	= make supports for dead-weight traps
26. de ne mo de saa	= make toys (like tinker toys)
27. de ne samba dufu	= make alcohol filtering device
28. gon kon bem	= cut the umbilical cord of newborns
29. hee ne ba-zu-tuwa	= make roof supports
30. sin ne kpare-nu-tuwa	= make door frames for house
31. sin ne kpare-nu a ko kundu	= make door of bush hut
32. tok ne te safi-tan	= stitch together to make a comb
33. de ne gbang	= cut into strips for ties
Uses of the panicle after threshing:	
34. de ne tong sowazi	= make local salt
35. de ne kpan-tong	= make bitter salt residue
36. a te wey o	= put in a fire as kindling fuel
37. foo ne nu bera	= clean the rim of a calabash dipper
Uses of the leaves:	
38. a ne dap toko	= extract purplish dye for coloring mats
39. mbaa ne mo	= wrap foods to prepare or store them
40. rami ne mo	= wrap things to carry them distances
41. 'bo ne kara	= wrap into a head cushion
42. 'bo kara nu ki'di	= wrap into a fish trap opening
43. de ne ki'di goro	= make entrance of beehives
44. de ne man, loo	= make into a play roller
45. ha duwa yong	= give to goats as food
46. hee ne gba-kiri	= wrap *gba-kiri* snacks
Uses of the root system:	
47. de ne kan vuwi 'doo	= use to stir beer or other beverages
48. de ne yina ko gok	= use to treat snakebite

TABLE 1. Continued.

Uses of the plant as a whole:	
49. dafa te, kana te	= use to curse someone or swear by
50. to ne wen	= refer to it in talk (proverbs, etc.)

youth at one instance. In order to retain his categories and his exact wording, the list of uses is presented in the same form as he offered it (Table 1), with translations provided on the right. A fuller account and further analysis of the place of sorghum in Suma life is the subject of another study (Bradshaw, 1986).

For almost all of the primary uses, there are ready substitutes in the Suma environment. Perhaps the clearest example relates to the use of the panicle for making local salt. Roger Sillans found as many as 25 different species used to extract plant salt in one location in the CAR (Prioul, 1981), and the Suma use at least 10 species, including cotton and sesame stalks, to obtain salt.

Substitutes for uses of the sorghum stalk are also readily available from such crops as maize and sugar cane as well as from wild *Andropogon* spp. As for the leaves, dyes are now purchased from Muslim boutiques. A wide assortment of plants are available to wrap things, make into head cushions, or build beehives, and children prefer to make rolling targets out of roots, not sorghum leaves. Goats do not depend on sorghum leaves for food, and goat pens made of sorghum stalks are not very sturdy. The root system makes an ideal, but not at all necessary, stirring stick; as a snakebite cure it has many competitors. The young plant serves as a powerful symbol with which to curse one's enemies, but blacksmith hammers and many other objects are considered to have an equally devastating effect. The Suma are such masters of curses that they derive their names (for different groups) from their favorite ones: "May a snake bite you!"; "May a lion claw your mouth!"; "May a hard spear enter your side!"—all of which need no symbol to accompany them.

USES OF SORGHUM CEREAL: THE PREDOMINANCE OF BEER

The various drinks made from sorghum differ considerably in strength and reputation. The least alcoholic ones are often referred to as "pastor's brew" (Protestant). The strongest drink, *harge*—the Suma equivalent of moonshine—is made with the hulls and other waste products from the first pounding of the grain. These ingredients can sometimes be found for sale in the market (Bell, unpubl.). Many Suma women distill *harge* and sell it to generate income.

Estimates for a related group in Cameroon (Burnham, 1980) indicate that one batch of distilled liquor can earn women from 1,500 to 2,000 CFA (roughly $4–5) after investing only about 500 CFA. This might represent as much as 3% of the average yearly income of such households (Burnham, 1980).

For *harge* to come out well, spouses must not quarrel during its preparation. Wives will frequently offer the first batch to their husbands' friends for free, but usually after carefully mixing it with reserves from old, well-rated batches to assure its initial acceptance. If anyone disapproves of it they can make comments such as "whiskers of a panther have gotten into this liquor." Since the whiskers and teeth of panthers are thought to be used for malicious purposes, such comments are suggestive of possible poisoning (Nangbei, unpubl.).

In the past, *'dungba* (*Nauclea latifolia* Sm.) bark bits were frequently added to enhance its taste. Now *nivaquine* (i.e., any medicine in pill form) sold in stores is often substituted. This is done to increase sales or to make it more attractive to temporary field workers who are offered *harge* as a reward for helping with cash crops. Although very strong, it is said that a good batch keeps the workers busy from dawn to dusk with no complaints. Farmers are very proud when many people come out to enjoy the partylike atmosphere of working and drinking all day in their fields (Nangbei, unpubl.).

Sorghum wastes were more commonly used for this drink when they were the natural by-product of processing grain into flour. Now that manioc is used for flour, the peels and other wastes from preparing the new staple have become the more common ingredient of *harge* liquor. The production of *harge* is thus a use of sorghum that has slowly declined as manioc became the Suma

staple. Presently, however, wastes of both manioc and sorghum are often used together to make *harge*.

The folklore associated with the liquor has remained intact. In this case the reason seems clear. The beliefs are associated with the process of making liquor and are relevant to the liquor itself, not to the plant that provides its ingredients. The same rules apply; thus spouses must behave courteously toward one another whether the wife is making sorghum or manioc liquor.

Sorghum pearls, as well as wastes, are used as trap bait. It is interesting that while sorghum crops are susceptible to the raids of several animals, the animals are likewise susceptible to being caught by the Suma precisely because they are attracted to the fields. For the Suma there are only two categories of food of overriding importance: staple dough and meat. Sorghum crops provide the first but also attract the second. An owner of a sorghum field who spotted monkeys in it from a distance would often quietly back off and return quickly to his village. There, he would announce publicly that he "had put manioc root in water to soak." Since this is a woman's task, his kinsmen would know the real meaning to be that he had spotted a group of red *patas* monkeys hiding in a tree near his field to eat his sorghum grain. The men would leave late that night and encircle the monkey hideout in readiness to kill a majority of them at dawn when they became visible. The yield of meat was probably an even match for the loss of grain caused by the monkeys, and the grain served to fatten the monkeys for the huge feast that inevitably followed. Nevertheless it seems unlikely that sorghum would ever be planted only because of its attraction to animals. Suma children spend days on end guarding the fields from predators, and from an early age they learn to set their first traps (usually snares) on the perimeter of their family sorghum fields. They also learn to use sorghum wastes to attract birds to locations at which they have set other kinds of traps, as this short excerpt from the memories of one informant shows (Bradshaw, unpubl. data).

> There was a young boy named Gboto who was a circumcision mate . . . who knew how to catch little *be-zer* birds with *genggele* traps. One day he showed Nangbei how to make these traps and catch these birds as he did. The *genggele* trap was a small cage made of *seere* branches [*Propsis africana* (Guill. & Perr.) Taub]. He set it up at a location where the *be-zer* birds were known to frequent; in a place where there were sorghum wastes lying around on the ground which served as bait. The birds could easily enter a cage but it was not easy to get out. So when a few had gathered inside, Gboto would quickly rush out from his hiding spot nearby and run to the cage to close up the entrance.

The attraction of birds, locusts, and other predators to sorghum may have favored the adoption of manioc, the underground tuber of which is more secure from predation.

Kuru fon is the name given to sorghum pearls that are eaten after boiling the seeds in water several times in succession. The softened grain (often combined with beans) is eaten as fast-food while working in the fields. A condition known as *ngasila-ngmgbong* (usually described as a painless swelling on the inside of the cheeks) is treated by chewing on once-boiled sorghum pearls and letting the dry flour of the center spread over the inner area of the cheeks. As the patient does this, another person asks him to explain what he is doing, to which he replies (Nangbei, unpubl.): "*Kuru ngasila-ngmgbong ye m yong he*" (literally, "It's boiled sorghum seeds that I'm eating for my cheeks"). This ritual has remained intact, but the use of the grain as a snack food or as a treatment for this particular illness is of minor value. Wild yams and fruits are abundant, and most ailments usually have a variety of widely known treatments.

It is sorghum-based beer, *bilibili,* and its less alcoholic counterparts, such as *lo'boto* that are considered essential. In a study conducted among the Gbaya of Cameroon, who have a maize-based beer and related drinks, 12% of the average (cash or barter) expenditures were used to purchase "beverages other than milk—mainly native beer and mead" (Burnham, 1980).

That sorghum beer itself has a large number of uses has been noted by several scholars writing about the CAR. Cordell (1977) describes the uses of millet beer in the CAR for: 1) offerings after a harvest, 2) libations dedicating new weapons, 3) offerings for fertility of newly cleared land, 4) bringing good fortune to a newborn child, 5) blessings at a new village site, 6) offerings by widows to deceased mates, 7) general tributes during mourning, and, of special note for this study, 8) rewards to workers engaged in group labor. Most of these apply to the Suma with reference to sorghum beer. Gosselin (1972) says that matrimonial relations begin with the request by the father of the young man, who offers some sorghum beer. Refusal to drink constitutes a re-

fusal of the alliance. The study of Gosselin (1972) focusing on work and social change in Gbeyaland is unfortunately of very uneven quality, offering both useful and misleading ideas about the use of sorghum beer. He notes that the Gbeya were initially suspicious of money and that sorghum served as their base of exchange. Leaders of so-called major lineages are described as being able to draw on the collective labor of their lineage community to work for them. They are said to entice men from nearby villages and "allied lineages" to join the work force by offering *lokpoto,* or sorghum beer. A reciprocal type of aid practiced between major lineages is called *ndefi,* according to Gosselin (1972). Although his description of collective work undertaken and the fact that sorghum beer is instrumental in the process is helpful, his analysis is weakened by the fact that the Gbeya do not have the lineage structure that he claims they do. Burnham (1980) makes it clear that Gosselin is mistaken in this regard. The fact is that while sorghum is certainly used to attract a labor force necessary to cultivate cotton as well as subsistence and/or cash crops (such as sesame), all farmers are free to offer beer when and where they so desire. The months of June and July are very busy for ambitious farmers, since the timing of cotton cultivation chores coincides with some of the subsistence crop chores. Furthermore, the money received from the previous harvest is all spent by this time of the year and very little food reserves remain by planting time. Manioc, which theoretically can be harvested at any time, is not easy to process during this period due to the rains that make it hard to sun dry, as is always done after soaking and pounding the root. Sorghum beer helps to make this very trying time of year a little less troublesome by providing sustenance, attracting labor, and promoting parties. If sorghum beer has important social functions throughout the year, it is at this time that it is most appreciated.

Burnham (1980) describes the role of maize beer among the Gbaya and suggests that the large amounts spent on beer do not constitute a serious drain on Gbaya resources because the cost of the beer, a small amount of money, mostly circulates within the community. Women take turns making it and men take turns paying for it, so it also has the effect of redistributing income in favor of women (Burnham, 1980).

Burnham (1980) clearly describes the Gbaya switch to growing maize in cash crop quantities as economically inspired, brought about by the demand for maize in Cameroon at the time. If the maize beer made by the Gbaya he describes is used in most of the same ways that sorghum beer is used among the Suma or other savanna peoples (cf. Cordell, 1977; Gosselin, 1972), it would demonstrate the fact that beliefs carry over with remarkably little trouble from one plant, or its products, to another.

Continuity Within Change: Yams, Game Meat, and Sorghum

When the Suma owner of a field has harvested his sorghum, he gives prescribed portions of the harvest to each of several special relatives who are present. The names of these harvest portions do not, however, describe any part of the sorghum plant but rather signify portions of game meat. One explanation for this might be that sorghum was introduced among the Suma when they were primarily a hunting and gathering people and that as new farmers they adapted the key terms used in hunting ritual for their sorghum harvest distribution ritual. These portions of the harvest, or gifts, are called *gore fon.* They are distributed very much like pieces of shared meat after a hunt. The sister of the sorghum's owner claims the *kokoto sa'de,* a preferred portion. The *gee sa'de,* or neck of the animal, is usually claimed by a uterine nephew while the *tan sa'de* (animal head) is usually reserved for the father or mother. When these close kinfolk are not present, other real or fictive kinsmen may advance their own disputable claims to special shares for themselves. Sorghum crops continue to be divided up this way even now that manioc is the staple. The manioc harvesting is done gradually, as needs for flour arise.

Before sorghum appeared on the scene, yams were probably the staple starch of the Suma. The roots were pounded into flour, and the form in which the food was served was undoubtedly as a staple dough. Sorghum was pounded in almost the same way and served as a staple dough. Sorghum adopted harvesting rituals associated with game meat distribution, but the form in which it was eaten carried over from yams. The processing was simplified somewhat, since sorghum did not have the alkaloids often found in yams that necessitated repeated washings.

As game meat becomes more scarce in this modern era, ritual once specific to its distribution will continue to be practiced in reference to

another staple. For a description of how game meat distribution ritual has been adopted to the modern practice of hunting with rifles, see Gosselin (1972). For information on the transfer from yam to sorghum to manioc in the CAR savanna, see Prioul (1981).

Summary

The study of cultivated plants should include as a necessary component a thorough examination of the uses made of the plants other than for food production. In the case of sorghum in Sumaland, the degree to which it is now cultivated has little relation to its present contribution to the year-round Suma diet. It may play a role in providing considerable sustenance at a critical time in the agricultural cycle when the planting of subsistence and cash crops coincides with the time of year (June–July) when other foods are less available, but it has a more important role in providing the means by which labor can be compensated in a society where cash income is low.

The social aspects of sorghum beverage consumption are not clearly distinguishable from the economic ones, the consumption of beer on the part of Suma men having the effect of increasing the amount and speed of cash circulating within the community. The compensation of temporary field hands with beverages allows almost any farmer to cultivate several hectares of cash crops, but also has significant social dimensions.

The non-food-related uses made of sorghum by the Suma appear to be tied directly to the use of its grain for making beverages. They demonstrate to what degree the Suma derive a large part of their material resources from agricultural byproducts. It may be of interest for ethnobotanists to concentrate more on the various secondary uses of food plants and to determine the alternatives to such uses. In less bountiful environments than Sumaland, there may be fewer alternatives and therefore more dependence on these secondary uses—in the Sahel for instance.

As the economic base of Suma society shifted from hunting toward sorghum culture (in association with yam culture and considerable gathering, no doubt) and then away from sorghum to manioc in the 19th century, Suma ritual and belief have found ways to adapt themselves to these fundamental changes. The division of the initial harvest of sorghum crops today reflects the age-old distribution ritual for hunted game, and the flour and wastes of relatively recently introduced manioc have taken on the functions and lore of sorghum products. Manioc is now served in exactly the same form as the flour of sorghum was served, as a pasty dough accompanied by sauces. Sorghum, in turn, may have been prepared this way when it was adopted because wild yams were originally prepared in the same manner.

It is apparent that the Suma have been flexible and open to quite radical alterations in their economic base, yet the age-old "conservative nexus" [Philip Burnham (1980) uses this term ("conservative nexus") in reference to the Gbaya and has also described the ecology of Gbayaland as "permissive"] of the society, the fundamental core of its unique ethnic character, has shown a remarkable stability in the case of plant lore. The few examples provided in this paper with regard to sorghum and manioc only allude to a more general phenomena whereby plant lore is adapting to the realities of a quickly changing world. Plant preparations once used for hunting accidents are now used for traffic accidents in the city, and the traditional charms for luck in hunting become charms for luck in urban employment. As was seen in the case of *harge* preparation, sometimes modern medicines—drugs in pill form—are substituted for plant-derived liquor enhancers. This can be very undesirable. Yet this too indicates the degree to which traditional moonshine distillation adapts quickly to modern markets.

The urban dweller today certainly knows far less than does his country cousin about the wide variety of plant uses in the rural environment, but the essential components of the system carry over to the urban environment. For example, the informant who earlier in this paper quickly listed the 50 uses of sorghum was a young man living in the nation's capital.

Traditional beliefs regarding plants do not usually inhibit a savanna farmer in the CAR from taking advantage of what appears to him to be economically advantageous. If, as has sometimes been suggested, African farmers neglect to grow more of a given cash crop because of sentimental attachment to bananas, for instance, it is almost certain that the sentiments in question have a sound economic footing and that too much dependence on a cash crop often results in long-term economic disadvantages (von Clemm, 1964). A Suma farmer who grows sorghum today does so not because he is very attached to the

crop but because it is very necessary from an economic point of view as much as any other.

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RELATIONSHIPS BETWEEN WOOD RESOURCES AND USE OF SPECIES FOR CONSTRUCTION AND FUEL IN THE COMMUNAL LANDS OF ZIMBABWE[1]

B. M. Campbell and R. F. du Toit[2]

Abstract

The use of woody species by peasant households in Zimbabwe has been investigated through household questionnaire surveys. The vegetation of the study area consists of miombo and mopane woodlands. A remarkably small number of species was recorded as being commonly used for fuel and construction. There are a few differences between species use for firewood and for construction, but only very minor variation in species use for different fuel and construction purposes. Most of the dominant species of the woodlands appear to be suitable for fuel and construction, partly because the unsophisticated rural technologies do not call for woods of very particular qualities. The species selected are generally the dominants of the climax vegetation even though the study area is severely deforested. This relationship occurs largely because of the nature of succession and deforestation in the miombo and mopane woodlands. However, in more deforested areas a different range of species is generally used and there are trends toward more indiscriminate use of species and greater use of introduced species. Since an advanced stage of deforestation was already reached in most areas over 20 years ago there has been little change in species use over this period.

Résumé

L'utilisation d'espèces ligneuses par les foyers paysans du Zimbabwe a été étudiée à travers des études basées sur des questionnaires chez l'habitant. La végétation de l'aire étudiée consiste en régions boisées de miombo et mopane. Très peu d'espèces ont été enregistrées comme étant régulièrement utilisées pour la construction et comme combustible. Il y a quelques différences entre les espèces utilisées comme combustible ou pour la construction, mais il y a des variations mineures entre les espèces employées pour des besoins differents comme bois de chauffage ou comme matériel de construction. La plupart des espèces dominantes des régions boisées semblent convenir comme combustible et matériel de construction, en partie parce que les techniques rurales simples ne requièrent pas de bois de qualités très particulières. Les espèces selectionées restent les dominantes de la végétation naturelle potentielle bien que la région d'étude soit sérieusement déboisée. Ce rapport est dû en grande partie à la nature de la succession et du déboisement dans les régions boisées de miombo et de mopane. Cependant, dans des régions où le déboisement est plus avancé une variété d'espèces assez différente est utilisée et on tend à y choisir les espèces avec plus de soin et à y employer un plus grand nombre d'espèces introduites. La plupart des régions en étaient déjà à un stade avancé de déboisement il y a plus de 20 ans, ce qui explique le peu de changement dans le choix des espèces durant cette période.

According to recent surveys, wood fuel comprises almost 50% of Zimbabwe's total energy consumption, and 99% of peasant households use wood for fuel (O'Keefe & Munslow, 1984; du Toit et al., 1984). Wood is also important in the construction of rural homes and fencing. For instance, about 50% of peasant households use wood in hut walls and over 90% use wood in roofs. Wood resources are no longer readily available in all areas, and about half the respondents in the survey of du Toit et al. (1984) said that wood was hard to obtain. A similar percentage said that the situation had worsened during the last 20 years.

The objective of the present paper is to describe the wood species used by peasant households for fuel and construction purposes and to relate species use to the resource base, i.e., to vegetation type and degree of deforestation.

Study Area

The study area comprises the group of communal lands in which the Rural Afforestation

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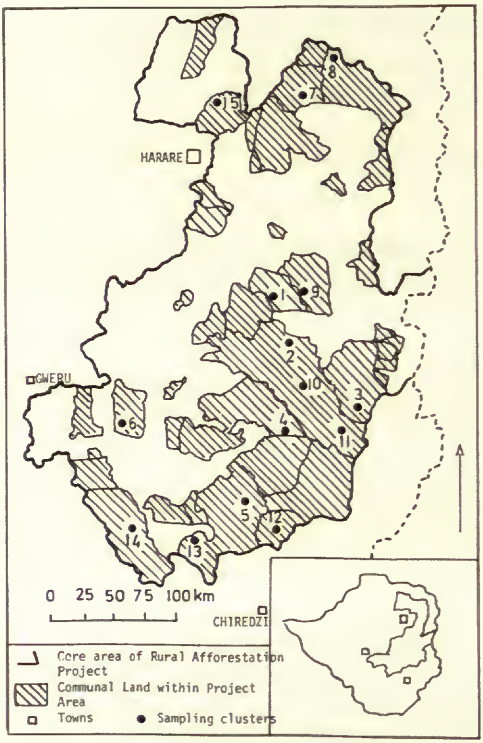

FIGURE 1. The 15 sampling clusters. Inset shows the study area in Zimbabwe.

Project is being implemented (Fig. 1). This project is aimed at the development of forestry in areas with severe wood deficits (Forestry Commission, 1982). The communal lands, in which the peasant sector is concentrated, can generally be described as being severely deforested, mostly as a result of the clearance of land for cultivation (du Toit et al., 1984).

The vegetation of the study area is predominantly miombo woodland in various stages of degradation. The dominant trees of the climax woodland are *Brachystegia spiciformis, B. boehmii,* and *Julbernardia globiflora.* A small portion of the study area (the area generally receiving less than 500 mm annual rainfall) is mopane woodland, dominated by *Colophospermum mopane* and less degraded than the miombo woodland, since cultivation is not so widespread in these drier areas.

METHODS

Data on species use were derived from a questionnaire survey of 1,829 households. The survey was done at 15 sampling clusters (Fig. 1). There were three to four sampling areas per cluster, giving a total of 58 sampling areas, each of which covered about 25 km^2. In the survey respondents were asked to name the tree species most commonly used by the household for various purposes, both at present as well as 15–20 years ago. The wood uses for which the questions were asked pertained to firewood (cooking and heating, beer brewing, baking bricks) and construction wood (hut walls, hut roofs, fencing). A proportion of the surveyed households did not engage in activities such as brewing and brick-making, and some respondents could not identify particular species that their households used (hence sample sizes in the tables do not equal the total number of households that were surveyed).

Aerial photographic analysis of the 58 sampling areas enabled the assessment of recent woodland cover (in the period 1978–1981) and past woodland cover (in the period 1957–1967). Each sampling area was classified into one of six classes of present woodland cover. Class 1 consists of areas that are least deforested. They have on average less than 20% of the land under cultivation and more than 50% of the land with open to closed woodland. Class 6 consists of sampling areas that are severely deforested, having on average over 50% of the land under cultivation and less than 10% of the land with open to closed woodland. Each sampling area was also classified according to the degree of change in its woodland cover over the period of study (roughly two decades). Further methodological details can be found in du Toit et al. (1984).

Sampling clusters were classified into three broad ecological zones, mainly on the basis of Wild & Barbosa's (1967) vegetation map of Zimbabwe and Vincent & Thomas's (1960) natural (agro-ecological) regions of Zimbabwe. The three zones—Highveld, Middleveld, and Lowveld—are primarily related to annual rainfall and altitude. Each zone has a characteristic combination of climax vegetation (see Table 2).

In addition to the above data, we have used information from three different tenure systems in the Condo area (near sampling cluster 2 in Fig. 1) to illustrate some specific aspects of species use in relation to deforestation. Of the three areas, the most deforested is the densely populated Sabi Communal Land; the sampling areas of the nearby sampling cluster fell into woodland cover classes 4–6. Both the small-scale commercial

TABLE 1. Major species used in all sampling areas for various purposes, at present and 15–20 years ago. The figures indicate percent households using a species. — = species used but with <1% frequency. Other species with less than 1.0% present use are listed in Appendix I.

	Cooking, Heating		Brewing		Baking Bricks		Wall Construction		Roof Construction		Fences	
	Present	Past	Present	Past	Present	Past	Present	Past	Present	Past	Present	Past
Brachystegia boehmii	28	32	29	29	19	20	17	19	11	12	9	11
Julbernardia globiflora	14	15	10	12	8	10	8	10	6	7	5	6
Colophospermum mopane	8	9	6	7	6	7	21	21	18	19	13	14
Brachystegia spiciformis	8	9	7	8	6	9	4	5	4	5	3	5
Combretum molle/apiculatum	8	7	6	7	5	5	4	4	4	4	5	5
Brachystegia glaucescens	6	7	6	8	7	8	4	4	3	4	3	4
Terminalia sericea	4	5	5	5	4	5	8	9	15	16	6	7
Sclerocarya birrea	—	—	—	—	2	2			—	—	—	—
Kirkia acuminata	—	—	—	—	2	1			—	—	—	—
Parinari curatellifolia	—	—	—	—	1	1	—					
Uapaca kirkiana	—	—	—	—	—	—	4	4	5	6	2	3
Pericopsis angolensis	—	—	—	—	—	—	—	—	1	1	2	3
Eucalyptus spp.	—					—			5	3	—	—
Diospyros quiloensis	—	—	—	—	—	—	—	—	1	1	—	—
Syzygium guineense/cordatum	—	—	—	—	—	—	—	—	1	1	—	—
Burkea africana	—	—	—	—	—	—	—	—	—	—	3	3
Any available species	17	7	22	13	30	21	23	13	23	8	38	28
Number of species recorded with <1% use	34	48	31	42	42	42	28	35	47	48	51	48
N	1,819	1,623	1,166	1,035	1,447	1,249	1,176	1,242	1,752	1,561	1,705	1,529

TABLE 2. Species use in relation to ecological zones and vegetation. The figures indicate percent households using a species. Only species used by more than 5% of households are shown. A—cooking and heating; B—brewing; C—baking bricks; D—wall construction; E—roof construction; F—fence construction.

	Highveld Miombo	Middleveld Miombo/Mopane	Lowveld Mopane/Miombo
Climax vegetation (Wild & Barbosa, 1967)	a) *Brachystegia spiciformis–Julbernardia globiflora* b) *Brachystegia boehmii–Julbernardia globiflora*	a) *Brachystegia boehmii–Julbernardia globiflora* b) *Julbernardia globiflora* c) *Colosphospermum mopane* d) *Terminalia sericea* e) *Brachystegia spiciformis–Julbernardia globiflora*	a) *Colophospermum mopane* b) *Julbernardia globiflora*
Dominant trees	a) *Brachystegia spiciformis* *Julbernardia globiflora* *Uapaca kirkiana* *Brachystegia glaucescens* b) *Brachystegia boehmii* *Julbernardia globiflora*	a) *Brachystegia boehmii* *Julbernardia globiflora* b) *Julbernardia globiflora* c) *Colophospermum mopane* d) *Terminalia sericea* *Burkea africana* e) *Brachystegia spiciformis* *Julbernardia globiflora* *Uapaca kirkiana* *Brachystegia glaucescens*	a) *Colophospermum mopane* b) *Julbernardia globiflora*
Natural region (Vincent & Thomas, 1960)	2/3	4/5	5

Sampling clusters (Fig. 1)	1, 7, 9, 15						2, 5, 6, 8, 12, 13, 14						3, 4, 10, 11					
Purpose: Species Used	A	B	C	D	E	F	A	B	C	D	E	F	A	B	C	D	E	F
Julbernardia globiflora	26	28	19	20	9	11	14	6		8	7	5						
Brachystegia boehmii	22	17	15	11	5	6	40	40	27	30	18	15	12	14	7			
Brachystegia spiciformis	15	11	9	6	6				7	7	5							
Brachystegia glaucescens	10	12	12	8	5	5	5							5	6			
Uapaca kirkiana				16	15	9												
Pericopsis angolensis						8												
Terminalia sericea					13		6	7	6	13	21	10					7	
Eucalyptus spp.					8						5							
Kirkia acuminata															8			
Diospyros quiloensis																	5	
Combretum molle/apiculatum													25	18	15	11	11	15
Colophospermum mopane										8	9	6	27	20	23	52	50	37
Any available species	17	21	31	29	24	42	17	20	33	21	16	41	19	26	25	23	17	30
N	489	275	416	253	461	450	850	598	695	537	819	791	474	291	338	382	462	457

farming area and the resettlement area have much climax miombo woodland. The data from the Condo area are only presented later in Table 7.

The accuracy of the questionnaire data depends on the certainty with which respondents can identify tree species. The botanical dictionary of Wild et al. (1972) lists scientific equivalents of vernacular names in Zimbabwe, and fewer than 0.5% of the trees named by respondents were not found in this dictionary. There is every indication that Zimbabwean peasants identify plants consistently (Wild et al., 1972). However, a vernacular name sometimes includes more than one species, which has been indicated as follows: *Combretum apiculatum/molle.*

Results

Tree species presently used

There are a few important differences between species use for firewood or construction, but only very minor variation in species use for different fuel or construction purposes (Tables 1, 2; Appendix I). The major species used are *Brachystegia boehmii, B. glaucescens, B. spiciformis, Julbernardia globiflora, Colophospermum mopane, Combretum apiculatum/molle, Terminalia sericea,* and *Uapaca kirkiana. Colophospermum mopane, U. kirkiana,* and *T. sericea* are used more frequently for construction purposes than for firewood, with *T. sericea* being particularly important in roof construction.

Species use for fence construction is particularly nonselective, with many respondents saying that their households used "any available species." This contrasts with some of the other activities to which far fewer respondents said that "any available species" were used (Table 1; cf. Table 2).

The majority of species used are indigenous. The most commonly used introduced tree is *Eucalyptus,* which is mainly selected for roof construction (Table 1). Other introduced species recorded include *Pinus* spp., *Melia azedarach,* and *Jacaranda mimosifolia.*

For each of the wood uses that were investigated, a total of only 35–60 species were named as the most commonly used species, and of these only 5–7 account for the answers from over 600 households. This lack of diversity is especially remarkable considering that the vegetation varies from miombo to mopane and that there are different types of miombo. We estimate that there are over 500 species of trees in the study area (excluding shrubs >2 m) (Drummond, 1975).

Table 3. Percentages of households, in different classes of woodland cover and in different classes of change in woodland cover, which cited different species as being commonly used for the two time periods investigated. Data for cooking and heating and roof construction (both these activities have large sample sizes).

	Classes of Woodland Cover		
	High Cover*		Low Cover†
	1/2	3/4	5/6
Cooking and Heating			
Change in woodland cover			
0‡	32	26	47
1	29	24	43
2	29	30	35
3	30	26	46
4§	no data	47	17
Roof Construction			
Change in woodland cover			
0‡	31	34	44
1	35	26	45
2	23	34	29
3	24	35	40
4§	no data	40	38

* Least deforested.
† Most deforested.
‡ No change.
§ Much change.

Species use in relation to vegetation type

The major factor affecting species use is vegetation type (Table 2) and is more important in determining species use than purpose to which wood is put. In Highveld the most frequently used species is *Julbernardia globiflora,* and it is only in this zone that *Uapaca kirkiana* was recorded as a commonly used species. In Middleveld the major species used is *Brachystegia boehmii,* with *Terminalia sericea* being more or less restricted to this zone. *Colophospermum mopane* is the most frequently used species in Lowveld, which is the only zone within which *Combretum apiculatum/molle* is commonly used. With a few exceptions, the major species used in the different ecological zones are generally the dominant species of the climax vegetation (Table 2). The only major species used that is not listed by Wild & Barbosa (1967) as dominant is *C.*

TABLE 4. Percentages of households, in different classes of woodland cover, using "any available species," rather than selected species, for various purposes.

	Classes of Woodland Cover					
	High Cover*					Low Cover†
Purpose	1	2	3	4	5	6
Cooking and heating	14	10	18	15	20	28
Brewing	16	15	21	22	26	32
Baking bricks	27	22	38	31	31	36
Wall construction	17	18	24	29	25	33
Roof construction	17	14	21	19	12	26
Fence construction	31	34	40	39	39	47

* Least deforested.
† Most deforested.

apiculatum/molle (in Lowveld). However, *Combretum* spp. are common in mopane woodland. *Brachystegia spiciformis* is a major tree of climax miombo woodland, particularly in Highveld, and yet it is not one of the most frequently used species.

It is perhaps surprising that in general the commonly used species are the dominants in the climax vegetation, because there is almost no climax vegetation remaining in the study area (e.g., 8 of the 15 sampling clusters average over 50% cover of cultivated land). The relatively close correspondence between species of climax vegetation and species use is related to the nature of deforestation and succession in the study area. The clearing of woodlands is patchy, and various stages of woodland degradation may be found in a small area. Furthermore, succession appears to follow the "initial floristic composition" model of succession, i.e., the species of the climax woodland are present even in pioneer and highly degraded communities (Drury & Nisbet, 1973). Thus the dominants of the climax vegetation are also the dominants in the degraded vegetation. The discrepancy between the dominance of *Brachystegia spiciformis* in the climax vegetation and its relatively low use is probably related to the low growth rates of *B. spiciformis*. In disturbed habitats the faster growing *Julbernardia globiflora* assumes dominance at the expense of *B. spiciformis* (Wild & Barbosa, 1967).

Most of the dominants of the woodlands appear to be suitable for fuel and construction. This is probably partly because the unsophisticated rural technologies do not call for woods of particular qualities. For instance, cooking appliances are rudimentary, being chiefly a metal grate, either fixed or portable, or simply a three-stone hearth (du Toit et al., 1984).

SPECIES USE IN RELATION TO DEFORESTATION

Table 1 indicates that there has been little change in species use between the two time periods investigated. All the major species used now were also the major species used 15–20 years ago, and the order of importance of the species

TABLE 5. Percentages of households, in different classes of woodland cover, using introduced species.

	Classes of Woodland Cover					
	High Cover*					Low Cover†
Purpose	1	2	3	4	5	6
Cooking and heating	0.0	0.0	0.0	0.0	0.3	0.3
Brewing	0.0	0.0	0.0	0.0	0.0	1.0
Baking bricks	0.0	0.0	0.0	0.0	0.0	0.0
Wall construction	0.0	0.0	0.0	0.0	0.0	0.0
Roof construction	1.4	1.7	1.1	4.3	12.4	9.7
Fence construction	0.4	0.7	0.0	0.6	1.8	1.5

* Least deforested.
† Most deforested.

TABLE 6. Percentages of households, in different classes of woodland cover and in different ecological zones, using particular species. Only species used by more than 5% of households in any woodland cover class are shown. Data for cooking and heating and roof construction (both these purposes have large sample sizes).

	Highveld Woodland Cover Class			Middleveld Woodland Cover Class			Lowveld Woodland Cover Class	
	High Cover*		Low Cover†	High Cover*		Low Cover†	High Cover*	Low Cover†
	1/2/3	4	5/6	1/2	3/4	5/6	1/2	4/5/6
Cooking and Heating								
Julbernardia globiflora	31	19	28	15	9	18	0	5
Brachystegia boehmii	13	30	25	45	52	29	12	12
Brachystegia spiciformis	10	19	20	8	7	7	1	5
Brachystegia glaucescens	14	7	6	7	4	3		
Terminalia sericea	6	3	0	10	4	4		
Combretum molle/apiculatum							27	23
Colophospermum mopane				1	2	5	37	16
Strychnos potatorum				0	0	5		
Any available species	17	18	13	10	16	24	12	26
N	190	198	90	226	277	347	241	233
Roof Construction								
Julbernardia globiflora	8	10	10	6	7	7		
Brachystegia boehmii	5	6	6	24	22	11		
Brachystegia spiciformis	6	7	5	6	4	4		
Brachystegia glaucescens	6	6	5	8	5	0		
Uapaca kirkiana	25	6	10					
Terminalia sericea	11	16	10	19	19	23	2	13
Eucalyptus spp.	5	7	21	0	0	13		
Colophospermum mopane				7	11	10	54	46
Syzygium guineense/cordatum	3	5	4					
Diospyros quiloensis							11	0
Combretum molle/apiculatum							13	8
Any available species	25	25	20	14	18	16	12	21
N	189	182	81	222	273	324	238	224

* Least deforested.
† Most deforested.

has not changed. An analysis of the percentage of households that cited different species as being important in the two time periods revealed no relationship with measured change in woodland cover; i.e., change in species use was not correlated with change in woodland cover (Table 3). The few changes that have occurred over the last two decades indicate that the natural woodlands are becoming even more degraded. Most of the preferred species are less frequently cited as being used at present, and there is now greater use of "any available species" (Table 1). Furthermore, the number of named species previously used is generally greater than the number presently used (even though sample sizes are larger for the recent time period). There are trends, therefore, away from the use of a variety of named trees and toward the use of "any available species." The relative lack of change in the use of trees during the last two decades is probably related to the relative lack of change in deforestation status in the last two decades; deforestation was already severe in the early 1960s (du Toit et al., 1984).

The more indiscriminate use of species with increasing levels of deforestation is clearly revealed in Table 4. There is also a trend toward greater use of introduced species in more deforested areas (Table 5, see Table 6 for *Eucalyptus*), and there appears to have been greater change in species use in the most deforested areas (Table 3). In Highveld there are no marked differences

TABLE 7. Percentage of households using particular species for fuel in the Condo area. Results based on three named species, in order of importance, from each household. Data weighted as follows: 1st choice—×3; 2nd choice—×2; 3rd choice—×1.

	Not Deforested		Severely Deforested
	Resettlement Area	Small-scale Commercial Farming Area	Communal Area
Julbernardia globiflora	45	36	14
Brachystegia boehmii	21	28	1
Brachystegia spiciformis	11	12	0
Terminalia sericea	7	11	8
Combretum molle/apiculatum	6	4	30
Colophospermum mopane	5	7	32
Brachystegia glaucescens	0	2	1
Strychnos madagascariensis	2	0	6
Dalbergia melanoxylon	0	0	2
Bridelia cathartica	0	0	4
Bauhinia thonningii	0	0	2
Other	3	0	0
Number of households surveyed	24	30	28

between species use in different woodland cover classes, except that *Uapaca kirkiana* is only important for roof construction in the least deforested areas, being replaced by *Eucalyptus* in the severely deforested areas (Table 6). In Middleveld there is much less use of *Brachystegia boehmii* in severely deforested areas (Table 6). This species is largely replaced by "any available species" for cooking and heating, and by *Eucalyptus* for roof construction. Showing a similar pattern to *B. boehmii* is the less frequently used *B. glaucescens*. *Colophospermum mopane* tends to be more frequently used in Middleveld areas in which deforestation is most severe. In Lowveld the patterns of use are complicated because the least deforested areas are also the areas that are predominantly mopane woodland as opposed to the mixed mopane/miombo woodland of the more deforested Lowveld areas.

These interactions between vegetation type and woodland cover class probably play a part throughout Table 6. The Condo data (Table 7), all collected from the same area with the same climax vegetation, allow for a more exact statement about change in species use as a result of deforestation. Households in the resettlement area and small-scale commercial farming area use very similar species for firewood, with *Julbernardia globiflora* and *Brachystegia boehmii* the most important species. Both areas have relatively good cover of miombo woodland. The pattern of species use is very different in the communal land because of the extensive deforestation. The most important species used for firewood are *Colophospermum mopane* and *Combretun apiculatum/molle*. There is some use of *J. globiflora* in this deforested area, but *B. boehmii* and *B. spiciformis* have almost completely disappeared as firewood. The species selection in the communal land reflects the vegetation that remains in the area—drainage line vegetation (*C. mopane* and *Combretum*) and trees remaining in the cultivated area (e.g., *Strychnos madagascariensis* and *Bauhinia thonningii*). That

TABLE 8. Some sacred tree species identified by community leaders (frequency of mention indicated).

Parinari curatellifolia	17
Strychnos spp.	8
Uapaca kirkiana	8
Ficus sur/sycomorus	6
Adansonia digitata	6
Afzelia quanzensis	3
Cordyla africana	3
Syzygium guineense/cordatum	3
Azanza garckeana	3
Diospyros mespiliformis/kirkii	3
Sclerocarya birrea	3
Brachystegia boehmii	2
Brachystegia spiciformis	2
Brachystegia glaucescens	2

TABLE 9. Mean percentage of households using fruit-bearing trees (averaged over the six wood uses).

	Classes of Woodland Cover					
	High Cover*					Low Cover†
	1	2	3	4	5	6
Uapaca kirkiana	1.7	3.5	3.3	1.5	0.7	1.4
Parinari curatellifolia	0.3	1.1	0.6	0.9	1.0	0.3
Sclerocarya birrea	0.2	1.0	0.8	0.1	0.1	0.4
Pseudolachnostylis maprouneifolia	0.1	0.4	0.9	0.6	0.4	0.2
Syzygium guineense/cordatum	0.3	0.2	0.7	1.0	0.3	0.2
Strychnos madagascariensis/innocua	0.2	0.4	0.0	0.4	0.0	0.1
Ficus glumosa	0.8	0.3	0.2	0.2	0.0	0.0
Diospyros mespiliformis/kirkii	0.1	0.3	0.0	0.2	0.1	0.7
Ficus sur/sycomorus	0.0	0.0	0.4	0.1	0.1	0.4
Strychnos cocculoides/pungens/spinosa	0.0	0.0	0.0	0.0	0.3	0.0
Berchemia discolor	0.0	0.0	0.0	0.0	0.0	0.1

* Least deforested.
† Most deforested.

such marked differences between woodland cover classes were not detected in the general data set is mostly due to the presence of a clear mosaic of mopane and miombo woodland in the Condo area. The miombo woodland is almost completely cleared for cultivation in the communal land, leaving mopane woodland along the nonarable watercourses.

SPECIES USE IN RELATION TO TRADITIONAL RESTRICTIONS

In conjunction with the major questionnaire survey, 31 supporting interviews with community leaders were conducted. When asked which trees were regarded as sacred, some of the community leaders cited particular species (Table 8), most of which are fruit-bearing trees. The *Brachystegia* trees mentioned were a few individual specimens that are held sacred (for example, specimens close to grave sites). Some community leaders simply stated that all fruit trees were sacred. The traditional restrictions on tree cutting do not appear to be strictly observed, as almost all the sacred species mentioned are used for wood. Munzwa (1979) observed that traditional restrictions varied according to the availability of wood. He recorded that in Zaka Communal Land a variety of tree species were taboo in the past (including *Burkea africana, Sclerocarya birrea, Flacourtia indica,* and *Pseudolachnostylis maprouneifolia*) but that these are now chopped almost indiscriminately. Table 9 indicates that there is not greater use of fruit-bearing trees in more deforested areas, except in the case of *Ficus sur/sycomorus, Berchemia discolor,* and perhaps *Diospyros mespiliformis/kirkii.* In general, patterns of species use cannot be related to traditional restrictions.

DISCUSSION

Species use appears to be primarily determined by degree of availability, with the more dominant species in the vegetation being the more frequently used species. There seems very little active selectivity. It is fortunate that most of the dominant species of mopane and miombo (occurring both in climax woodland and in highly degraded woodland) appear suitable for household wood needs. Eucalypt wood has been used for cooking by very few households, since it is not readily available in communal lands; but there is a general belief that it is not a good firewood species (du Toit et al., 1984). The results presented here suggest that this belief is unlikely to be a major problem in the acceptance of rural afforestation (which in Zimbabwe involves the establishment of eucalypt woodlots). In some sampling clusters as many as 35% of households use "any available species"; as soon as *Eucalyptus* becomes more available, it will be used more frequently by households.

It is difficult to compare the results presented here with other published results, because most ethnobotanical information is in the form of lists of species used, with little quantitative and ecological data. The only major work previously done in Zimbabwe is that of Whitlow (1979). He provides data on preference in relation to defores-

tation, but no actual data on the species selected is presented.

Liengme (1983) studied wood use in mopane vegetation in the northern Transvaal (R.S.A.). She predictably found that the two most commonly used species for firewood are *Colophospermum mopane* and *Combretum apiculatum* and that *C. mopane* was the most important construction wood. She also found that *C. mopane* and *Combretum apiculatum* were singled out by households as being the best firewoods. She states that "this would seem to indicate that the people are selective in their gathering of firewood," but she also goes on to say that the use of these species as firewood may simply be a result of their availability in the vegetation. As in our survey, she recorded the use of *Eucalyptus* for roofs, especially in the most deforested areas.

It has been argued elsewhere that the prime factor causing deforestation in Zimbabwe is cultivation (du Toit et al., 1984). Wood collection for fuel and construction is not as important as cultivation in the process of deforestation. Although the effect of wood collection on deforestation is limited, the converse is not the case. Deforestation status has a marked effect on wood collection, not only in terms of species used (this study) but also in such terms as time spent gathering and localities in which wood is available (du Toit et al., 1984).

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Appendix I

Species used by less than 1% of households (supplement to Table 1). Purposes: A = cooking and heating; B = brewing; C = brick baking; D = wall construction; E = roof construction; F = fence construction.

Acacia amythethophylla/nigrescens, ACDEF
Acacia nilotica/karroo/tortilis/others with straight white thorns, ABCDEF
Acacia schweinfurthii, DF
Afzelia quanzensis, ACF
Albizia adianthifolia/harveyi, ACF
Albizia antunesiana/versicolor, C
Artabotrys brachypetalus, F
Bauhinia petersiana, ABCDEF
Bauhinia thonningii, ABCDEF
Bequaertiodendron magalismontanum, E
Berchemia discolor, ACD
Breonadia microcephala, E
Bridelia cathartica, AF
Cassia abbreviata, ABCDEF
Cassine aethiopica, ADF
Celtis africana, ADE
Combretum fragrans, ABCDEF
Combretum hereroense, CE
Combretum imberbe, ABCDEF
Combretum zeyheri, DEF
Commiphora mossambicensis, ABCDEF
Crossopteryx febrifuga, AEF
Dalbergia melanoxylon, ABCDEF
Dalbergia nitidula, C
Dalbergiella nyasae, ACDEF
Dichrostachys cinerea, ABCDEF
Diospyros lycioides, DEF
Diospyros mespiliformis/kirkii, ABCDEF
Diplorhynchus condylocarpon, A
Ekebergia capensis, F
Erythrina abyssinica, F
Erythrophleum suaveolens, C
Faurea saligna/speciosa, ACDEF
Ficus glumosa, ABCDEF
Ficus sur/sycomorus, ABCDF
Flacourtia indica, C
Friesodielsia obovata, F
Grewia inaequilatera/monticola/bicolor, ABCDEF
Heteropyxis dehniae, C
Jacaranda mimosifolia, F
Lannea discolor, EF
Lonchocarpus capassa, BC
Maytenus senegalensis/heterophylla, ADEF
Melia azedarach, ABCE
Monotes engleri/glaber, ABCDEF
Ochna pulchra, C
Ozoroa insignis, E
Peltophorum africanum, ABCDEF

Pinus spp., AB
Protea spp., AC
Pseudolachnostylis maprouneifolia, ABCDEF
Pteleopsis myrtifolia, ACEF
Pterocarpus angolensis, DEF
Pterocarpus rotundifolius, CEF
Rhus chirindensis, CDE
Securidaca longipedunculata, CDEF
Strychnos cocculoides/pungens/spinosa, AC
Strychnos madagascariensis/innocua, ABCEF
Strychnos potatorum, ABCDEF
Swartzia madagascariensis, CEF
Tabernaemontana elegans, A
Terminalia prunioides, F
Terminalia stenostachya, CDEF
Trichilia emetica, EF
Vitellariopsis ferruginea, E
Xeroderris stuhlmannii, C
Zanha africana, E
Ziziphus mucronata, E

PLANTS IN TRADITIONAL MEDICINE IN WEST AFRICA

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Abstract

The utilization of plants in ethnomedicine is established by trial and error and it is believed that nature has indicated by evident signs how each plant is to be used. The traditional healers include the "Ifa" priests and the herbalists who employ two kinds of treatment (real and psychological). Herbal preparations may be in powder taken with pap or used in scarification; in concoction or decoction; may be pounded with native soap; prepared as rubbing ointment or in the form of soup. The traditional healers have found plant parts of *Annona senegalensis, Poterium spinosum,* and *Morinda lucida* efficaceous in the treatment of cancer. *Enantia chlorantha* and other plants have also been found effective in the treatment of malaria. *Rauvolfia vomitoria, Voacanga africana, Perquetina, Jatropha,* and numerous other species are used in ethnomedicine for the treatment of psychological and psychosomatic diseases. Frigidity in man might be arrested using parts of *Garcinia kola, Gossypium barbadense,* etc. Different recipes of anticonvulsant are reviewed. Other antiinfective and antimicrobial agents include *Ageratum conyzoides, Piper guineense, Xylopia aethiopica, Alchornea cordifolia,* and *Zanthoxylum zanthoxyloides.* Plants used as rituals are also discussed. In West Africa a Bioscience Network has been set up to look into the possibility of establishing an Institute of Traditional Medicine.

Résumé

L'utilisation de plantes en ethnomédecine est établie par tâtonnements et on pense que la nature indique par des signes évidents comment on doit utiliser chaque plante. Parmi les guérisseurs traditionnels se trouvent les prêtres et les herboristes "Ifa" qui utilisent deux sortes de traitement (réel et psychologique). Des préparations aux herbes peuvent être des poudres absorbées dans des bouillies ou utilisées en scarification; en concoction ou décoction; peuvent être pilées avec du savon indigène; préparées sous forme de pommade ou de soupe. Les guérisseurs traditionnels ont découvert que des parties d'*Annona senegalensis, Poterium spinosum,* et *Morinda lucida* sont efficaces pour le traitement du cancer. On a trouvé qu'*Enantia chlorantha* et d'autres plantes sont utiles pour traiter la malaria. *Rauvolfia vomitoria, Voacanga africana, Perquetina, Jatropha,* et de nombreuses autres espèces sont utilisées en ethnomédecine dans le traitement de maladies d'origine psychologiques ou psychosomatiques. On peut stopper la frigidité masculine en utilisant des parties de *Garcina kola, Gossypium barbadense,* etc. Les auteurs examinent diverses recettes d'anticonvulsif. D'autres agents anti-infectieux et antimicrobiens comprennent *Ageratum conyzoides, Piper guineense, Xylopia aethiopica, Alchornea cordifolia,* et *Zanthoxylum zanthoxyloides.* Les plantes utilisées pour les rites sont aussi mentionnées. En afrique occidentale un Réseau Bioscientifique a été créé afin d'examiner la possibilité d'établir un Institut de Médecine Traditionnelle.

The use of plants by early man was established by trial and error. Plants eaten by animals and not resulting in fatality were soon adopted by man as food and sometimes as medicinal plants. In West Africa, before mushrooms are eaten, they are first fed to chickens; if pecked, they are assumed as consumable. This is still the practice in rural areas, where rudimentary identification has not been perfected. Thus plant parts causing irritation or inflammation in contact with the skin are soon identified and may be used as a counterirritant. Plants that induce vomiting or purging are used in treating food poisoning and indigestion, and others that cause sweating are found to reduce fever.

Apart from such usages based on the observation of direct effects, the employment of plants as medicaments is mostly empirical, and frequently infused with a strong element of magic. It is often thought that nature had indicated by evident signs how each plant was to be used. Thus a plant with leaves lobed like the liver was useful in disease of that organ, a plant with heart-shaped leaves was of value in cardiac disturbances. Plants growing among broken rocks and supposed to disintegrate them would have a similar action on stones in the bladder. Plants with swollen or bulbous roots might be used to check emaciation.

With all the advances in modern and orthodox medicine, traditional medicine is still very much alive and plays an important role in health care

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in West Africans. Recent developments in pharmacology are, however, providing a basis for their evaluation and exploitation.

Treatment Modalities of Traditional Healers

In West Africa, the traditional healers include the Ifa priests and herbalists. They employ two kinds of treatment, real and psychological. Real treatment is for those who require no incantation or other ceremonies, while psychological treatment is for those who do require incantation or other fetish ceremonies such as sacrifices before the medicine can be effective. The plant parts commonly used include fruits, leaves, stem, and root barks. When harvested they are usually sun dried for preservation for subsequent sale in herb markets.

Herbal preparations come in various forms: (i) Powder, which can be swallowed or taken with pap. (ii) Scarification, which involves powdered plant material rubbed into cuts made on any part of the body with a sharp knife or blade. (iii) Herbs may also be soaked for some time in water or local gin before drinking. This is then decanted as required. They may also be boiled with water. (iv) Pounded with native soap and given to the patients for bathing. (v) Pastes, pomades, or ointments in a medium of either palm oil or shea butter (*Butyrospermum paradoxum*). These are rubbed into the affected parts of the body. (vi) Preparations may also be taken as a soup.

Medicinal Plants Used in Folkloric Medicine

ANTICANCER

The word cancer is foreign to traditional healers. It is often diagnosed as abnormal swelling. The Biochemistry Department and the College of Medicine of the University of Ibadan and their counterparts in Ghana are carrying out active research on anticancer agents in collaboration with traditional healers. Healing with plant recipes has been confirmed by research scientists. The best results so far have been obtained with *Annona senegalensis, Poterium spinosum,* and *Morinda lucida.*

A crystalline material isolated from the stem of *Morinda lucida* has been shown to exhibit a carcinostatic effect on Sarcoma 180 ascites in mice (Durodola, 1974). Durodola (1975a) has also isolated and purified a constituent of the root of *Annona senegalensis,* measuring its antineoplastic activity against Sarcoma 180 ascites tumor cells. At the optimal daily dose of 100 mg/kg intraperitoneally (i.p), the active material designated C/M_2 has a potent antitumor effect, with 100% tumor inhibition, prolongation of survival for 60 days or more, and no toxicity to the host. Ether extracts of the root bark of *Poterium spinosum,* a plant used in folkloric medicine for treating diabetes mellitus, has also been screened (Durodola, 1975b). A crystalline material isolated from the extract has an oncolytic effect on Sarcoma 180 ascites in mice, while an amorphous material obtained in the same extraction was devoid of antineoplastic activity.

ANTIMALARIA

Malaria is one of the major and most common killing diseases in West Africa, accounting for 90% of infant mortality. Treatment may be in the form of concoction, decoction, steam for inhaling, and powder used with pap. Stem bark of *Enantia chlorantha* in local gin is one of the most popular treatments for malaria. For the steam treatment where the patient is subjected to the vapors from boiling herbs, the ingredients include leaves of *Azadirachta indica, Carica papaya, Mangifera indica, Cymbopogon citratus, Citrus aurantifolia,* and *Psidium guajava.* Stem bark of *Alstonia boonei* soaked in water also has an antimalaria action. Other plants used include *Khaya species, Mitragyna inermis, Morinda lucida,* and *Nauclea latifolia.*

The Ghanaian herbalists have found that a concoction of the root bark of *Cryptolepis sanguinolenta,* which occurs in Senegal, Sierra Leone, Guinea, Ghana, and Nigeria, is effective in the treatment of malaria (Soladoye et al., unpubl.). Based on the traditional use, Oku-Ampoto (Director of Scientific Research into Plant Medicine in Ghana) tested this clinically and suggested that it may have some potential as an antimalarial drug. Boye (pers. comm.) also supported this view. Gillert et al. (1951) isolated a major alkaloidal constituent, crypto-lepine, and demonstrated that it caused a pronounced lowering of blood pressure in dogs as well as the lowering of body temperature. It is at present being processed by the West African Pharmaceutical Federation (WAPF) for clinical application. According to John Ocran, the Executive Secretary of WAPF (pers. comm.), the potion is presently being used to treat malaria and rheumatism at the Scientific Research Centre, Plant Medicine, Mampong, Ghana.

As indicated earlier, a lot is being done to screen some of the plants listed above by West African research scientists. In *Alstonia boonei,* echitamine appears to be the most active constituent pharmacologically. The detailed autonomic pharmacology of echitamine has been investigated in some laboratory animals (Ojewole, 1983). The alcoholic extract of *Azadirachta indica* leaves and stem bark yielded nimbolide, margosine, nimbidin, nimbin, and nimbosterol and showed antiinflammatory effects (Okpamyi, 1977). The boiled leaf extract exhibits antimalarial and antilymphocytoxic properties which may be of clinical use in lymphocytic proliferative disorders such as lymphomas and leukemias. The schizontocidal activity of an aqueous extract of *A. indica* has also been reported (Ekanem, 1983).

Stem bark of the four species of the Mahogany genus—*Khaya ivorensis, K. anthotheca, K. grandiflora,* and *K. senegalense*—are used as fever remedies in localities where they grow. *Khaya senegalensis* and *K. ivorensis* produce many limonoid bitter principles (Adesina, 1983b).

Decoctions or infusions of *Mitragyna inermis* are sudorific, diuretic, and have antirheumatic properties. Apart from quinovic acid and sitosterol reported earlier, *M. inermis* was found to produce indole, oxindole, and heteroyohimbidane oxindole alkaloids in different parts of the plant (Shellard & Sarpong, 1970).

Various parts of *Morinda lucida* are used for many ailments, and the plant is considered antimalarial, astringent, antipyretic, purgative, refrigerant, diuretic, and anthelmintic. Leaf, bark, and/or root decoctions are drunk for all forms of fever, jaundice, and constipation. Adesogan (1973) discussed the chemical analyses.

The root, stem, and leaves of *Nauclea latifolia,* as with all other known potent antimalarial drugs, are bitter. The leaves yielded a total of 0.08% of alkaloids, including naufoline and augustine, also present in the root bark (Hotellier et al., 1975).

PSYCHIATRIC AND PSYCHOSOMATIC DISEASES

In most African societies, mental illness is seen as a clear manifestation of a disturbed equilibrium of life. The disease may be traced to broken taboo, contravened societal norm, or witchcraft. It is indeed futile to prescribe herbs and tranquilizers without first making a proper diagnosis of the cause of the illness. Treatments often include sacrifices, rituals, and dances. The use of herbs is only secondary to the spiritual or magical cure of insanity. The improvement in the healing of mental illness was generated by the advent of *Rauvolfia* alkaloids (Iwu, unpubl.).

In many West African villages and towns, traditional doctors build hospitals mainly for the treatment of mental patients. A tablespoon of powdered root bark of *Rauvolfia vomitoria* mixed with local gin is given three times daily as a cure for mental disorder (Kio et al., 1984). *Voacanga, Parquetina,* and *Jatropha* are among the common ingredients in medications for insanity.

Several psychosomatic disorders are traced only to gods, evil spirits, and the magic manipulations of enemies. Such possessed individuals exhibit aberrant behavior that can be mistaken by a layman for insanity. Cure can only be effected after the appropriate ritual sacrifices and other religious acts are performed. Among the herbs used for the preparation of medicine used in the treatment of psychosomatic disorders are *Abutilon grandifolium, Acacia macrothyrsa, Achyranthes aspera, Asparagus africana, Cajanus cajan, Celosia hastata, Commelina africana, Rauvolfia vomitoria, Terminalia spinosa, Leucaena leucocephala,* and *Oncoba spinosa.*

LIBIDO PROMOTING HERBS

Exploitation of the "libido factor" is nothing new in West Africa. The sales of Guinness beer rocketed in Nigeria after a series of advertisements hinting broadly that it gave men something extra. In Ghana, in the days when foreign drinks could still be bought, the sale of Campari and soda was promoted on a racy advertisement, thus suggesting that it was an aphrodisiac.

In traditional healing, *Garcinia kola, Gossypium barbadense* (fruit), and camphor ground into powder and mixed with honey has been found effective as a cure for frigidity. Fruit of *Musa sapientum* (sliced and dried) ground and stored in honey has also been found to be a good recipe. A concoction of fresh leaves of *Sida urens* is used by traditional healers in some parts of Nigeria. Other ingredients include the roots of *Monodora tenuifolia, Acanthus montanus, Carpolobia lutea, Sphenocentrum jollyanum, Tricalysia subcordata, Memecylon afzelii,* and leaves of *Blepharis maderaspatensis.*

ANTICONVULSANTS

The use of indigenous anticonvulsant remedies is as old as the recognition of convulsions. Though the herbalists did not comprehend the detailed chemical, biochemical, pharmacologi-

TABLE 1. Phytochemical analysis of selected *Solanum* species from West Africa. Negative (−), positive (+), and trace (±).

Plant Species	Part	Alkaloids	Saponins	Flavonoids	Tannins	Coumarins Isolated and Identified
S. aethiopicum L.	Ripe fruit	+	±	+	−	Scopolin
	Leaf	+	±	−	−	Scopoletin Scopolin
S. americanum Jacq.	Leaf	+	+	+	−	Scopoletin Aesculin Scopolin
S. gilo Raddi	Unripe fruit	+	+	+	−	Scopoletin
	Fruit					Scopoletin
	(green variety)	+	+	+	−	Scopolin Isoscopoletin
		+	+	−	−	Scopoletin
S. macrocarpon L.	Unripe fruit	+	±	−	−	—
	Leaf	+	±	−	+	—
S. melongena L.	Root	+	+	−	±	Scopoletin
	Fruit					Scopolin
S. nigrum L.	Unripe fruit	+	+	+	−	Scopoletin
	Leaf	+	+	+		Scopoletin Scopolin Aesculin
S. torvum Swartz	Root	+	+	−	−	—
	Ripe fruit	−	±	−	−	Scopoletin Aesculin Scopolin
S. scabrum L.	Leaf	+	+	−	±	Scopoletin
	Ripe fruit	±	−	+	−	Aesculin Scopolin

cal, and nutritive values of their medications, years of committed observation, long practice, and loyalty usually made for some success (Adesina, 1983a).

The management or control of convulsions in West Africa is achieved through the use of herbal concoctions alone or concoctions of plant, animal, and/or insect parts. Such preparations may contain rock salt, black alum, metal salts, and sulfur. Substances with demulcent and lubricant properties such as shea butter, palm oil, and palm kernel oil may be added. Three such anticonvulsant preparations are prepared from the following items:

Recipe A. *Nicotiana tabacum* (leaves), *Citrus medica* (fruit), *Tetrapleura tetraptera* (fruit), *Xylopia aethiopica* (fruit).

Recipe B. *Kigelia africana* (root or fruit), *Allium ascalonicum* (leaves), *Capsicum annuum* (fruit), sodium chloride.

Recipe C. *Portulaca oleracea* (leaves), *Talinum triangulare* (leaves), *Archatina marginata* (one giant snail), *Gossypium arboreum* (leaves).

These items are usually cut into small pieces, soaked in a medium of choice, and used prophylactically or during a fit.

Some remedies are made into soap form and patients suffering from convulsions can wash off febrile conditions and fevers thought to cause or precipitate such convulsive episodes. Two such remedies contain the following ingredients.

Recipe D. *Plumbago zeylanica* (root), *Xylopia aethiopica* (fruit), *Allium ascalonicus* (leaves), native soap.

Recipe E. *Olax subscorpoidea* (root), *Allium ascalonicum* (leaves), native soap, driver ant (*Dorylus* spp.), musk, rat with offensive odor.

Recipes D and E are separately ground together and used topically in washing off febrile conditions.

SOLANACEOUS PLANTS AS ANTICONVULSANTS

Many *Solanum* species have been found very effective in the management or control of convulsions in Nigerian ethnomedicine. Most of

these are sources for vegetables and edible fruits. They are also employed as tonics, antirheumatics, and remedies for colds, fevers and dizziness.

Adesina et al. (unpubl.) have investigated some species of Nigeria *Solanum* (Table 1).

The relative amounts of coumarins and steroidal alkaloids are important when one considers the relative toxicity or potency of the indigenous anticonvulsant preparations. While the fruits of *Solanum aethiopicum* and *S. gilo* are usually eaten raw, the fruits of *S. melongena* are steamed first. Fruits of *S. torvum, S. macrocarpum, S. scabrum,* and *S. americanum* are not eaten at all except in medicine. Only the leaves of *S. aethiopicum, S. americanum, S. macrocarpum, S. nigrum,* and *S. scabrum* are usually boiled and eaten as a vegetable. *Solanum scabrum,* which appears to be the most toxic as evidenced by the behavioral tests, is also the most promising anticonvulsant drug.

OTHER ANTIINFECTIVE AND ANTIMICROBIAL AGENTS

Ageratum conyzoides. It is common practice among young people to use the leaves of *Ageratum conyzoides* (Compositae) for minor cuts. A liquid extract is applied to the cut, which is then covered with leaves. Within a few days the cut is healed. The herb is widely used in Africa, India, and many others part of the world to treat wounds and ulcers. In some places it is used to treat gonorrhea. Fractions of petroleum ether extract of the stem have been tested for antibiotic activity against *Staphylococcus aureus.* Its healing property was also tested on live rabbits. The fractions that showed greatest activity against *S. aureus* were also most effective in promoting wound healing (Adesogan, 1983).

Piper guineense. Piper guineense (Piperaceae), also known as West African black or Ashanti pepper, has traditionally been used in the treatment of coughs, gastrointestinal disorders, colds, bronchitis, venereal disease, and rheumatism. It is also used as spice in foods, in suppositories for its medicinal properties, and as a preservative in indigenous medicinal preparations. The findings of Hänsel et al. (1966), Hänsel & Zander (1961), Hänsel & Petter (1969), and others justify the use of all parts of *Piper guineense* by herbalists in the treatment of infectious disease (Adesogan, 1983).

Xylopia aethiopica. Xylopia aethiopica is a common ingredient in medicine in West Africa. Work by Boakye-Yiadom & Dwuma-Badu (1977) confirms its preservative property, which may account for the reason it is commonly used. It has also been demonstrated by the same workers that the crude extract and three pure diterpines, including xylopic acid, from the fruits of *Xylopia aethiopica* are active against *Bacillus subtilis, Pseudomonas aeruginosa,* and *Staphylococcus aureus.* Xylopic acid was also found to be active against the fungus *Candida albicans.* Aqueous decoctions of the fruits of *X. aethiopica* are used in Ghana to remove round worms (Dwuma-Badu, 1983).

Alchornea cordifolia. Decoction of the leafy twigs is used as an application to sore feet and as a lotion or poultice (Dalziel, 1937). The pulverized dry leaf is applied to ulcers and yaws. Leaf extracts have been found to inhibit the growth of bacteria such as *Staphylococcus aureus, Staphylococcus albus,* and *Escherischia coli* (Ogunlana & Ramstead, 1975).

Zanthoxylum zanthoxyloides. Root powder is applied to gums for about five minutes, and the use of roots as chewing sticks is reported to hasten healing (Kio et al., 1984). The antimicrobial property of the chewing stick has been investigated by El-Said et al. (1971; see also Lewis & Elvin-Lewis, 1977). For sore throat, salt is added to powdered root bark and two tablespoonfuls are taken in warm or cold water twice daily. For gonorrhea or urinary antiseptic, root bark is soaked in sterile water for twelve hours, and a tablespoonful of resulting solution is taken three times daily.

Enantia chlorantha. The antimalaria properties of *Enantia chlorantha* has been discussed above. The species occurs in Ghana, Nigeria, and other parts of West Africa and is used traditionally for treating ulcers, leprous spots, and jaundice. The analgesic, adrenocorticotrophic, and antibacterial activity of the alkaloids may be responsible for the effective use of the plant in the treatment of jaundice, a condition that can be produced by viral or bacterial infection of the liver, resulting in infective hepatitis. The use of the plant in treating wounds and skin diseases is attributed to the antiinflammatory, analgesic, and antibacterial action of the alkaloids present.

PLANTS USED IN RITUALS, CUSTOMS, AND TABOOS

Newbouldia laevis, commonly grown as a live fence, is often found around groves and shrines, along with *Dracaena, Erythrina,* and *Jatropha curcas.* The leaves of *N. laevis* are used in tra-

ditional chieftaincy rituals during the installation ceremony. The leaf is put in the cap of the appointed chief, leaving part of the blade exposed. This symbolizes his appointment as the chief or "oba," thus allowing him all rights and privileges associated with the title.

Palm fronds (*Elaeis guineense*) are usually used for warning signs. Split leaves tied across a path leading to the bush indicates that nobody should enter the bush to cut sticks. This sign is common on fallow bush about to be cleared for farming. To ensure good representation in a society meeting, this sign is kept across the entrance into a village to prevent delinquent members from going out.

Shrines are usually decorated with palm fronds to keep away evil spirits. It is also common practice to put a palm frond outside the vehicle conveying a human corpse to counter evil spirits. Fronds may also be placed in the grave to prevent the reincarnation of a wicked man. Dried and ground *Chasmanthera dependens* used with native soap for bathing in a stream will counteract the effect of evil spirits invoked by cursing. The same plant with the ground fruit of *Butrospermum paradoxum* is used for the treatment of fractures. The fruit of *Adenopus breviflorus* in water and placed in a room will minimize the spread of smallpox during an epidemic. Leaves of *Rauvolfia vomitoria* are used to bathe a woman who looses her child shortly after birth and have been found effective to minimize future losses. *Euphorbia latifolia* planted round a building will drive away the forces of evil spirits.

Okoubaka aubrevillei, which occurs in Bendel State, Nigeria, Ivory Coast, and in some other parts of West Africa, is very rare. In Ivory Coast, it is known to kill neighboring plants, except *Myrianthus arboreus* and *Musanga cecropioides,* by exuding poisonous liquid from its foliage at sunrise and sunset. (Visits to Sapoba Forest Reserve, Benin, Bendel State in Nigeria confirmed also the presence of *Barteria fistulosa* and *Draceana* species as associated species but not *Musanga.*) The bark of *Okoubaka* is often used in making charms to drive evil from a house.

In West African universities, research into herbal medicines is being carried out. In the Faculty of Pharmaceutical Sciences, traditional medical practitioners are usually employed to supply herbal recipes. It is hoped that with time herbal medicine will provide cure to the diseases that are resistant to modern drugs. In West Africa, a Bioscience Network has been set up to look into the possibility of establishing an Institute of Traditional Medicine.

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EAST AFRICAN PLANTS USED IN BASKETRY[1]

CHRISTINE H. S. KABUYE[2]

ABSTRACT

Before the introduction of synthetic materials, people in East Africa used (and in many areas still do use) a good number of plant materials for basketry. Basketry, which most likely started with hunter-gatherers wanting to carry the gathered roots, fruits, etc., to their base, has over the years developed into an intricate craft. The first basket was probably made of a wide leaf or group of leaves tied with a twiner. Basket forms today range from wickerwork using whole twigs, twilled baskets using strips of hard but more or less flexible branches or stems, woven baskets using bark and leaf fibers, plaited baskets using split or whole monocot leaves, to coiled basketry where a number of materials are used. Their sizes and uses are as varied. Plants used are commonly from the following families: Euphorbiaceae (especially *Acalypha*); Papilionaceae (especially *Indigofera*); Vitaceae for twigs and stems; Gramineae (especially Bamboo, *Pennisetum,* and other reeds); Palmae; and a few dicots for twilled basketry, including Tiliaceae, Malvaceae, Sterculiaceae, Bombacaceae, Moraceae, and Mimosaceae (especially the genus *Acacia* for whole bark or bark fibers); Agavaceae for leaf fibers; Palmae leaves for plaited basketry; Palmae, Marantaceae, Musaceae for coiled basketry. A number of plants are used for dyes to add color to the baskets, especially varying shades of yellow, brown, red, and black.

RÉSUMÉ

Avant l'introduction de matériel synthétique, les habitants de l'Afrique Orientale utilisaient beaucoup de matériel végétal en vannerie; ils le font d'ailleurs encore dans de nombreuses régions. La vannerie, qui est née probablement lorsque les personnes qui vivaient de chasse et de ceuillette voulaient emporter des racines, fruits, etc. jusqu'à leur campement, s'est transformée au cours des ans en un artisanat complexe. Le premier panier fut sans doute fait avec une grande feuille ou un groupe de feuilles liées par une brindille. Les paniers varient aujourd'hui des paniers en osier faits de brindilles entières, ou des paniers sergés utilisant des morceaux de branches dures mais plus ou moins flexible ou des tiges, et des paniers tissés en écorces ou en fibre de feuilles, jusqu'aux paniers faits de feuilles des monocotylédonées entières ou coupées, et aux paniers torsadés utilisant un matériel divers. La taille et l'utilisation de ces paniers varient. Les plantes les plus souvent utilisées proviennent des familles suivantes: les Euphorbiacées, surtout le genre *Acalypha*; les Papilionacées, surtout *Indigofera*; et les Vitacées pour les brindilles et les tiges; les Graminées, surtout le Bambou, le *Pennisetum,* et d'autres roseaux; les palmiers et un certain nombre de dicotylédonées pour les paniers sergés, y compris les Tiliacées, Malvacées, Sterculiacées, Bombacacées, Moracées, Mimosacées, surtout le genre *Acacia,* pour l'écorce entière ou les fibre d'écorce; les Agavacées pour les fibres de feuilles; les feuilles de palmiers pour les paniers tressés; les Palmées, Marantacées, et Musacées pour les paniers torsadés. Plusieurs plantes sont ulisées comme teintures pour colorer les paniers de teintes variables et principalement les jaunes bruns, rouges, et noirs.

Basket making in East Africa has a long tradition. It must have started when people wanted containers to carry or store collected food, and probably the first basket was a large leaf or a number of leaves tied with a vine. This simple requirement for containers has over the ages developed into a complex art with more and varied needs for containers both for home and open market. In fact, for some, basketry is a valuable occupation providing gainful employment.

In the African setting, basketry is an art passed on from mother to daughter or father to son, so there is a pattern followed in methods and materials used. A number of plants are exploited for basketry. The choice has a direct bearing on what materials are easily available, but durability is an important consideration. Thus when a desired plant is no longer available in the vicinity, people will travel far afield to search for or buy the required material. In recent times the introduction of sisal and the ease of obtaining synthetic fibers, dyes, etc., especially in the urban

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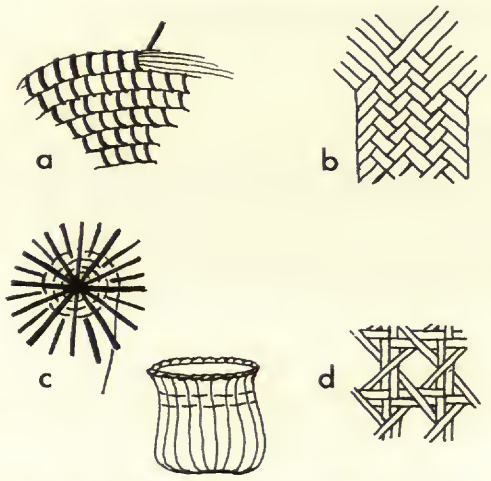

FIGURE 1. Methods of basket making.—a. Coiled.—b. Plaited.—c. Wickerwork.—d. Twilled.

areas, has cut down on traditionally accepted materials used in basketry. But many rural people still use traditional plant-derived materials.

The materials used range from whole stems, twigs, and leaves to stem, leaf, and root fibers, while a number of natural plant-derived dyes are used to give color to the articles made. An annotated list of the plants used is given in Appendix I.

There is a wide variety of baskets from small, almost decorative baskets to smooth food "bowls" and water-carrying baskets, as well as the rough ones for food harvesting, storage and winnowing, and fishing traps (Figs. 2–4).

Methods used are as varied, the more common being coiled, plaited, wickerwork, and open weaving, with a certain amount of twilled basketry.

In coiled basketry a bundle of the required thickness made of grass or fiber is formed and a flat strip, say from the palm leaflet, is lapped round the bundle through a hole in the previous coil. This way a continuous coil (Fig. 1a) is made until the article is finished. The hole is made with an awl or thorn such as obtained from *Acacia*.

Plaited basketry, mostly from palm leaves, is done in two stages. First the dried leaflets of young leaves are split into strips, although they can be used whole for rougher work. These are plaited (Fig. 1b) to make a long strip the required width. The strip is then joined coilwise using a durable fiber sewn through loops in the edges of the strips. The baskets so made can either be open and wide-mouthed with string for lifting or can be narrow-mouthed and have a cover made in the same way.

Wickerwork basketry is done by arranging split stems or twigs starwise, with another strip or twig going around them and alternating over one and under the next. The edge is finished by folding the ends over a flexible stick going around the rim (Fig. 1c). The rim is finished with a fiber.

Open weaving can be done like wickerwork but using fibers or it can be done straight without laying down the "star" and shaped later by sewing. The twilled basketry (Fig. 1d) is mostly found on chair seats and backs but simpler modifications of this are found.

It is mostly the monocots that are used for coiled basketry, but root strands of *Cissampelos mucronata, C. pareira,* and *Stephania abyssinica* (all Menispermaceae) are very important for the tribes in northwest Kenya. The roots are used for both the lapping strip and the thinner bundle components of very durable food and drinking bowls. The monocots involved in this class are *Marantochloa leucantha* and *M. purpurea* (Marantaceae) in Uganda. Culms of *Eleusine coracana* are important for the lapping strips in making neat food bowls and decorative baskets, especially in areas of East Africa where it is also grown as a crop. *Hyphaene coriacea* is one of the very important plants in basketry. The leaflets, either split or whole, are used in making water pots sealed with beeswax. Also made from the leaflets are the clothes baskets made by the Turkana for the open market. A strong fiber obtained from the upper surface of young *Raphia* palm leaves is used as a lapping strip in delicate and decorative baskets.

The bundle for the coils can be made from thin dried strips of *Musa* leaf midrib, thin culms of *Loudetia kagerensis* or *Eragrostis olivacea,* shredded fibers from palm leaves, or roots like those of *Asparagus flagellaris.*

Plaited basketry is mostly done with leaflets of palms, but other monocots can be used. The most commonly used are the two *Hyphaene, H. compressa* and *H. coriacea,* mostly in the north of Uganda, Kenya, and coastal Kenya. In other parts of Uganda and western Kenya, *Phoenix reclinata* is used. In some forms of plaited basketry strips are not made first and a number of sedges are used, including *Cyperus maranguensis, Mariscus luteus,* and *Rhychospora corymbosa,* which can be plaited into fine baskets.

For wickerwork basketry, which includes har-

FIGURE 2.—a. Eating table cover made in Tanzania from palm leaf rhachis, simple twilled.—b. Food cover made in western Uganda from split leaflets of *Phoenix reclinata,* coiled.—c, d. Grain-preparing baskets made in Tanzania from culms of *Eleusine* sp., coiled.—e. Delicate baskets made in western Uganda from *Sansevieria* sp., coiled.—f. *Kiondo* (storage basket) made by Kikuyu women in Kenya from bark fibers of *Dombeya* sp., open woven.—g. Food bowl made by the Tugen in Rift Valley, Kenya, from roots of *Cissampelos* sp., coiled.—h. Half-gourd-shaped eating bowl or basket for grain winnowing made by Pokot from strips of bamboo, wickerwork.—i. Water pot made by Dorobo in Kenya from bark fibers of *Dombeya* sp. and root strips of *Stephania abyssinica,* strong doubly coiled.—j. Pot stand made from *Cyperus papyrus,* twilled.

vesting, storage, some winnowing, and fishing baskets, the following are important: whole or split branches of *Acacia brevispica* (Mimosaceae), *Abrus precatorius, A. schimperi, Dalbergia commiphoroides, Indigofera spicata, I. swaziensis* (Papilionaceae), *Acalypha bipartita, A. fruticosa, Securinega virosa* (Euphorbiaceae), *Lawsonia inermis* (Lythraceae), *Sida acuta* (Malvaceae), *Combretum denhardtiorum* (Combretaceae), *Helinus mystacinus* (Rhamnaceae), *Canthium guienzii* (Rubiaceae), *Teclea nobilis* (Rutaceae), *Allophylus abyssinicus, A. africanus, Paullinia pinnata* (Sapindaceae), *Thylachium africanum* (Capparaceae), *Hippocratea* spp. (Celastraceae), *Jasminum abyssinicum* (Oleaceae), and *Secamone punctulata* (Asclepiadaceae).

For finishing the edges or tying together, whole bark fibers of the following are used: *Triumfetta* spp., especially *T. macrophylla* and *T. tomentosa, Grewia* spp., *Glyphaea brevis,* and *Dombeya* spp. Whole stems of *Cissus* spp. and *Cyphostemma adenocaule* (Vitaceae) can be used in making granaries. *Smilax kraussiana* (Smilacaceae) was chosen by the Kenya Tea Company for tea-picking baskets. Other monocots important in this class are also found in twilled basketry, discussed below.

For open woven baskets, apart from the introduced sisal (*Agave sisalana*) which has captured the market, the following are important for stem fibers: *Adansonia digitata* (Bombacaceae); *Abutilon longicuspe, A. mauritianum* (Malvaceae); *Acacia polyacantha* ssp. *campylacantha* (Mimosaceae); *Crotalaria* spp. (Papilionaceae);

FIGURE 3.—a. Carrying basket made in Uganda from leaf rhachis of *Eremospatha* sp., mixture of wickerwork and twill.—b. Carrying basket made in Uganda (but also common in western Kenya) from leaf rhachis of *Phoenix reclinata,* wickerwork. The edge is finished with whole bark of *Triumfetta* sp.—c. Unfinished open carrying basket made on Kenya coast from split leaflets of *Hyphaene compressa,* plaited.—d, g. Food-preparing baskets made by the Baganda in southern Uganda from *Marantochloa purpurea,* coiled.—e. Water pot made by Gabbra in northern Kenya from leaflets of *Hyphaene coriacea,* strong double coil.—f. Purse made on Kenya coast from leaflets of *Hyphaene compressa,* plaited.—h. Container with cover used as clothes basket made for the open market from *Hyphaene compressa,* combination of coil and twill.

Antiaris toxicaria, Ficus sycomorus, F. thonningii (Moraceae); *Sterculia africana, Dombeya* spp. (Sterculiaceae); *Corchorus olitorius* (Tiliaceae); *Pittosporum viridiflorum* (Pittosporaceae); *Gnidia subcordata* (Thymelaeaceae); and *Obetia pinnatifida* (Urticaceae). Relatives of the sisal in Agavaceae, *Dracaena* spp. and *Sansevieria* spp., are also used where they occur.

In twilled basketry (Fig. 1d) or simpler variations on this, strong materials are used. I have found that these are mostly in the families Gramineae and Palmae. Marantaceae and Cyperaceae are used to a lesser extent. Of the Gramineae, *Pennisetum purpureum, Phragmites mauritianus, Echinochloa pyramidalis, Saccharum spontaneum, Arundinaria alpina,* and *Oxytenanthera abyssinica* are invariably used for open or covered carrying baskets and baby baskets. These are made from split culms.

The palm *Eremospatha,* found in Tanzania and western Uganda, is used for chair backs and seats as well as for other fine basketry. Other palms including *Borassus aethiopum, Elaeis guineensis, Hyphaene* spp., *Phoenix reclinata,* and *Raphia* sp. are used for rough but durable baskets and some winnowing baskets. In these cases the outer part of the split leaf stalk and rhachis are used, while for finishing edges the inner part of the rhachis or other strong fibers are used. Stems of *Marantochloa* spp. can be used in the same way as the palm leaf rhachis. Stems of *Cyperus alternifolius, C. articulatus, C. papyrus,* and *Fimbristylis ferruginea* are used to make simple twilled baskets.

Another group of twilled basketry includes fishing baskets and traps. The long surface stolons of *Cynodon nlemfuensis* are used for fishing baskets, as well as the stems of *Flagellaria gui-*

FIGURE 4.—a, b. Decorative baskets made in Uganda from leaf fiber of *Raphia* palm, coiled (a, multiple coil).—c. Carrying basket made in central Kenya for the open market from *Agave sisalana,* open woven.—d, e. Carrying baskets made by the Akamba in Kenya from fibers of *Adansonia digitata,* open woven.—f. Skirt made by El Molo of Kenya from *Hyphaene coriacea* leaflets beaten to fibers between two stones, woven.—g. Open carrying basket made by the Turkana of northern Kenya from leaflets of *Hyphaene coriacea,* combination of coil and twill.—h. Purse made in Uganda from leaflets of *Phoenix reclinata,* plaited.—i. Fruit or wastepaper basket made from banana leaf-base fibers, coiled.—j. Bead basket with cover made in western Uganda from leaf fibers of *Raphia* palm, coiled.—k. Toy made from *Raphia* palm leaflets, coiled.—l. Container used as clothes basket made for the open market by the Turkana in northern Kenya from *Hyphaene coriacea,* coiled.

neensis and leaves of *Imperata cylindrica.* Fibers of *Securidaca longipedunculata* (Polygalaceae), *Pouzolzia hypoleuca* (Urticaceae), and *Dombeya cincinata* are used for fine ropes made into fishing nets.

The colors for basketry are derived from a number of plants (Appendix I). A few important examples are mentioned here. For red or red-brown: roots of *Adansonia digitata,* fruits and roots of *Rubia cordifolia,* leaves of *Lawsonia inermis,* roots of *Rumex abyssinicus,* roots of *Piliostigma thonningii,* and bark of *Rhizophora mucronata.* For brown: pounded bark of *Hymenocardia ulmoides,* bark of *Harungana madagascariensis,* stem and leaves of *Maesa lanceolata,* bark of *Avicennia marina,* and bark of *Ficus sur.* For black: roots and leaves of *Euclea natalensis,* ripening fruits of *Anacardium occidentale,* bark of *Syzygium guineense,* and whole plant of *Cycnium jamesii.* For yellow: bark of *Combretum molle* and *Terminalia brownii,* boiled leaves of *Maerua pubescens,* flowers of *Portulaca foliosa,* bark of *Annona chrysophylla* and *Mangifera indica.* It is also reported that a blue dye can be obtained from pods and seeds of *Piliostigma thonningii* and from ash of *Commiphora samharensis.*

APPENDIX I

Plants used in basketry, including their common names and specific uses.

DICOTYLEDONS

Acanthaceae

Thunbergia alata L. Mkunguzi (Swahili).—A red dye is made from the crushed plant.

Amaranthaceae

Gomphrena globosa L. Mseche (Giriama).—A red dye is made from the crushed plant.

Anacardiaceae

Anacardium occidentale L. Cashewnut, Mkanju (Swahili).—A black dye is obtained from the ripening fruits.

Lannea humilis (Oliv.) Engl.—Common in Karamoja, Uganda, where the bark fiber is chewed to make string woven into women's underskirt.

L. stuhlmannii (Engl.) Engl. Muyumbu (Swahili), Wahari (Boni), Mukivure (Giriama).—The bark is steeped in water and warmed to produce a red and brown dye used to color palm leaves, etc.

L. triphylla (A. Rich.) Engl. Taboyo (Pokot).—The bark fiber used the same way as for *L. humilis*.

L. sp. Nyoldokh (Rendille).—The branches used for panniers to carry water containers.

Mangifera indica L. Mango.—The pounded bark produces a yellow dye used for dying basketry fibers.

Annonaceae

Annona chrysophylla Boj. Mbokwe (Swahili and Digo).—A yellow or brown dye is obtained from the bark.

Uvaria kirkii Oliv.—A black dye is obtained from the roots.

U. scheffleri Diels. Mukukuma (Kamba), Mulkusho, Tamuketio (Pokot).—The thin branches are used for granaries; the bigger branches used for the frame of panniers for carrying water containers.

Apocynaceae

Landolphia buchananii Stapf. Ntapajit (Dorobo).—Provides a strong rope used in tying.

Saba comorensis (DC.) Pichon (syn. *S. florida*). Ikolko (Dorobo).—The switches are used for building granaries in Karamoja.

Asclepiadaceae

Dregea abyssinica (Hochst.) K. Schum. Ndepepet (Dorobo).—A fiber is obtained from the stems.

D. schimperi (Decne.) Bullock. Latelesi (Dorobo).—A fiber is obtained from the stems.

Periploca linearifolia Dill. & Rich. Muimbaigoro (Kikuyu).—Stems used for tying as in the following species.

Secamone punctulata. Juchunga (Dorobo), Engoilei (Masai), Kibraluma (Kipsigis).—Stems mostly used as a fiber for making the frame for huts by Masai and Kipsigis.

Bignoniaceae

Stereospermum kunthianum Cham. Mufumbiri (Digo).—The bark provides fiber.

Bombacaceae

Adansonia digitata L., the Baobab. Mbuyu (Swahili), Mwamba (Kamba), Ol-imisera (Masai), Njau (Boni).—Fiber is obtained from the inner bark and made into string used in carrying baskets (Kiondo) by the Akamba. A red dye is obtained from the roots.

Rhodognaphalon schumanianum A. Robyns. Mparamusi, Msufi mwitu (Swahili).—A reddish-brown dye is obtained from the bark.

Boraginaceae

Cordia africana Lam. Ibolinga (Dorobo).—Fiber is obtained from the bark.

C. sinensis Lam. (syn. *C. gharaf*). Edome (Dorobo).—Fiber is obtained from the inner bark and used for tying sticks in the framework for huts in Turkana.

Burseraceae

Commiphora samharensis Engl. Nderotwa (Pokot).—A blue dye is obtained from the ash of this tree.

Caesalpiniaceae

Brachystegia spiciformis Benth. Mriti (Swahili), Nkuti (Rungwe).—The inner bark is made into a fiber.

Cassia floribunda Cav. Mugusa (Maragoli).—Fiber from the bark is used for finishing edges of winnowing baskets.

Piliostigma thonningii (Schumach.) Milne-Redh. Mukolokolo (Kamba), Mchikichi (Swahili).—The roots macerated and boiled produce a red to brown dye while a blue dye is obtained from the pods and seeds. The bark fiber is made into cord and used to make *kiondo* (woven baskets) by the Akamba in Kenya.

Capparaceae

Maerua pubescens (Kl.) Gilg. Mukasi (Swahili).—A yellow dye is made from boiled leaves.

Thylachium africanum Lour. Mdudu, Mtunguru (Swahili).—The straight young stems are used for granaries.

Celastraceae

Hippocratea africana (Willd.) Loes. Toropchiot (Dorobo).—The stem is used as a rope.

H. indica Willd. Tonoyal (Pokot).—The stem is used as a rope in making fishing baskets by the Pokot.

Combretaceae

Combretum denhardtiorum Engl. & Diels.—The twigs are used for wicker baskets.

C. molle G. Don. Mukungo (Taita).—A yellow dye is obtained from the bark.

Terminalia brownii Fresen. Ipokoi (Dorobo).—A yellow dye is obtained from the bark.

Compositae

Carthamus tinctorius L.—Flowers are a source of a yellow dye.

Connaraceae

Agelaea heterophylla Gilg (syn. *A. obliqua* (Beauv.) Baill.). Miugu, Kikuyu.—Stem used to make winnowing baskets (coiled type).

Ebenaceae

Euclea natalensis DC. ssp. *obovata* F. White (syn. *E. fructuosa*). Mauth (Boni), Mdaa-mwitu (Swahili).—Leaves are boiled to make a black dye, also obtainable from the roots.

Euphorbiaceae

Acalypha bipartita Muell. Arg. Omukagati (Ankole).—The stems are used in making wickerwork carrying baskets.

A. fruticosa Forssk. Etetelaik (Turkana), Olando Makwar (Luo), Edindi (Luhya).—Stems are used to make a wickerwork shield in Turkana, white ant traps in Karamoja, and elsewhere for winnowing, carrying, or food-storing baskets.

Euphorbia reinhardtii Volkens. Rumiri (Pare).—Gum from the stem is used to seal the wickerwork winnowing baskets.

Hymenocardia acida Tul.—A red-tan dye is obtained from the bark.

H. ulmoides Oliv.—A brown dye is obtained from the pounded bark.

Phyllanthus muellerianus (O. Ktze.) Exell. Mkumbu (Swahili).—The bark produces a black dye when boiled in water and a brown dye when pounded and put in cold water.

P. reticulatus Poir. Mzizima (Swahili).—The roots produce a black dye.

Securinega virosa (Willd.) Baill. Mkwamba (Swahili & Giriama).—Split stems and branches make strong wickerwork baskets on the Kenya coast.

Hypericaceae

Harungana madagascariensis Poir. Funa Maji (Swahili).—A brown dye is obtained from the pounded bark and an orange dye from the red sap of the stem.

Labiatae

Fuerstia africana T. C. E. Fr.—A red dye is obtained from the leaves.

Lauraceae

Cassytha filiformis L.—The stems are pounded and mashed in water to produce a brown dye.

Lythraceae

Lawsonia inermis L. Muhena (Swahili), Esajait (Turkana), Halan (Rendille).—A red dye is obtained from the leaves, especially on the coast. The stems are used by the Rendille for making panniers for carrying water containers. The Turkana use the stems for frames of fishing baskets.

Woodfordia uniflora (A. Rich.) Koehne.—The flowers produce a dye.

Malvaceae

Abutilon longicuspe A. Rich. Mondwe (Kikuyu), Leldingiyet (Dorobo).—Fiber is obtained from the bark, once used for open woven baskets by the Kikuyu and still used by the Dorobo.

A. mauritianum (Jacq.) Medic. Sulubei (Dorobo), Lukusa Lusecha (Bukusu).—The bark is used for baskets.

Hibiscus spp.—Many species provide a good bark fiber invariably used in different kinds of baskets, finishing edges of wickerwork winnowing, carrying and storage baskets, and joining strips for plaited baskets. The following are commonly used.

H. aponeurus Sprague & Hutch. Mikuma (Meru).
H. cannabinus L.
H. diversifolius Jacq.
H. furcatus Roxb.
H. fuscus Garcke
H. panduriformis Burm. f.
H. rostellatus Guill. & Perr.
H. tiliaceus L. Mtakawa (Swahili).

Sida acuta Burm. f. Tsinundu (Kisa).—Twigs are used for hen house made in wickerwork fashion.

S. ovata Forssk.—Fiber from the bark.

S. rhombifolia L.—The Dorobo use the fiber in making baskets.

Pavonia patens (Andr.) Chiov.—The fiber is used in basketry by the Dorobo.

P. urens Cav. var. *tomentosa* (Ulbr.) Brenan.—The fiber is used by the Dorobo.

Urena lobata L. Sulubei (Dorobo), Owich (Luo), Mpuruza (Swahili).

Menispermaceae

Cissampelos mucronata A. Rich. Olandra (Luo), Tabararet (Kipsigis).—Strands obtained from the root used for small coiled-type food basket.

C. pareira L. var. *orbiculare* (DC.) Miq. Molutwo (Endo).—Strands are made from the roots and used in making the small coiled type food bowls made by the Endo and Tugen.

Cocculus hirsutus (L.) Diels.—Fibers are used in basket chairs. A black dye is obtained from the roots and dry fruits mixed with clay.

Stephania abyssinica (Dill. & Rich.) Walp. Tabaret (Kipsigis).—The fiber is used as a binder for basket edges, and the root fiber is used in making the small deep coil-type food baskets and drinking bowls by the Tugen.

Mimosaceae

Acacia spp.—A number of these are exploited for fiber that can be utilized in basketry.

A. brevispica Harms. Osiri (Luo).—The straight branches are used for a fishing basket frame, with papyrus and *Triumfetta* being used as the fibers.
A. elatior Brenan ssp. *turkanae* Brenan. Esanyanait (Turkana).—Thorns are used as a needle in coil basketry or for sewing.
A. gerrardii Benth.—A string is obtained from the inner bark.
A. hockii De Wild.
A. polyacantha Willd. ssp. *campylacantha* (A. Rich.) Brenan. Mugu (Kikuyu).—The bark fiber is woven into open baskets by the Kikuyu.
A. senegal (L.) Willd. Mugaa (Kikuyu).
A. tortilis (Forssk.) Hayne ssp. *spirocarpa* (A. Rich.) Brenan.

Moraceae

Antiaris toxicaria (Pers.) Lesch. Mkunde (Digo).—The white bast fiber is woven into bags by the Digo.
Ficus sur Forssk. (syn. *F. capensis*).—The bark is pounded to give a brown dye.
F. sycomorus L. Mukuyu (Taita).—The inner bark is chewed, and string made from it is woven into open baskets.
F. thonningii Blume. Mvumu (Taita).—The inner bark used as in the preceding species.

Myrsinaceae

Maesa lanceolata Forssk.—A brown dye obtained from the sap in the stem and leaves.

Myrtaceae

Syzygium guineense DC.—The bark yields a black dye.

Oleaceae

Jasminum abyssinicum R. Br. Embugu (Kigezi).—Stems are used for wickerwork baskets in western Uganda.
J. fluminense Vell. Epelech (Turkana).—Stem produces string.

Papilionaceae

Abrus precatorius L. Mkandume (Swahili).
A. schimperi Hochst. Egagate (Kisukuma), Mseati (Kilua), Muitha (Kamba).—Stems of the above two species are used for wickerwork baskets, especially by Akamba, and for fishing baskets.
Crotalaria spp.—A number of *Crotalaria* species yield fiber used by Kikuyus for basket weaving.
Dalbergia commiphoroides Bak. f. Daiya (Somalia).—The twigs are used in making panniers for carrying water containers.
Indigofera spicata Forssk. Olando (Luo), Kabambamaliba (Luganda).—The stems are used for making bird traps.
I. swaziensis Bolus. Mucugucugu (Kikuyu).—Stems used in wickerwork baskets and winnowing baskets.
Vatovaea pseudolablab (Harms) Gillett. Henadi (Rendille).—The roots produce fiber.

Phytolaccaceae

Phytolacca dodecandra L'Herit. Wasowasit (Dorobo).

Pittosporaceae

Pittosporum viridiflorum Sims. Kijulu (Taita).—The roots are chewed to produce white fiber used in weaving baskets by the Taita.

Polygalaceae

Securidaca longipedunculata Fresen.—Produces fiber made into string for fishing nets.

Polygonaceae

Rumex abyssinicus Jacq. Mugagatio (Kikuyu), Omuka (Ankole).—A red-brown dye is obtained from the roots and used to dye raffia fiber in Uganda. The dye is used to color *Dombeya* and *Hibiscus* fiber for open baskets by the Kikuyu.

Portulacaceae

Portulaca foliosa Ker-Gawl. Borori (Boni).—The flowers provide a yellow dye.
Talinum portulacifolium (Forssk.) Schweinf. Leshurshin (Dorobo).—Provides a dye.

Proteaceae

Protea angolensis Welw.—The bark is pounded to give a brown dye for winnowing baskets.

Rhamnaceae

Helinus mystacinus (Ait.) Steud. Loitegomi (Dorobo).—Twigs are used for wickerwork baskets by the Dorobo.
Rhamnus prinoides L'Herit.—Berries are made into a red dye.
Zizyphus mauritiana Lam.—A cinnamon-colored dye is obtained.

Rhizophoraceae

Rhizophora mucronata Lam. Mkoko Msinzi (Swahili).—The raw bark is pounded in cold water, then left for three days to produce a reddish-brown dye.

Rubiaceae

Canthium gueinzii Sond.—Stems are used for wickerwork baskets.
Rubia cordifolia L. Kasalabakesi (Luganda).—The species yields a red dye from ripe fruits. Palm leaflets and grass are steeped in the dye and dried before weaving. In Uganda, a dark red dye for raffia fiber is obtained from the roots.

Rutaceae

Teclea nobilis Del.—Branchlets are used in wickerwork granary construction.

Santalaceae

Osyris abyssinica A. Rich. Kijulu (Taita).—A white fiber is obtained fom the roots and used in open woven baskets.

Sapindaceae

Allophylus abyssinicus (Hochst.) Radlk. Mutete (Ankole, Lukiga and Luganda).—The thin branches of this species and the following are used in wickerwork basketry.
A. africanus P. Beauv.—Like *A. abyssinicus*, its branches are used for wickerwork baskets.
Paullinia pinnata L. Wananda (Luo), Orutarabugo (Ankole).—The stem is used as rope in making fish traps.

Sapotaceae

Afrosersalisia cerasifera (Welw.) J. H. Hemsley. Malvahoya (Shambaa).—A reddish dye is obtained from the bark boiled in water.

Scrophulariaceae

Cycnium jamesii (Skan) O. J. Hansen.—A black dye is obtained from the whole plant for dying palm leaflets.

Sterculiaceae

Dombeya burgessiae Gerr. & Harv. (syn. *D. nairobensis, D. mastersii*). Amakhambi (Kisa), Mukeu (Kikuyu).—The stem produces the best fiber for string. The inner bark produces thread used to finish edges of basket work and trays used by the Kikuyu.

D. cincinnata K. Schum.—Stem fiber is used for making nets.

D. goetzenii K. Schum. Iborgwai (Dorobo).—The fiber is used to make baskets and bow string.

D. rotundifolia (Hochst.) Planch. Ndowa (Taita).—The stem produces fiber used in making baskets in Taita.

Sterculia africana (Lour.) Fiori. Moria (Giriama), Mtakea (Swahili).—The stem produces fiber for making basket handles and rope.

S. rhynchocarpa K. Schum.—The bark produces fiber.

Thymelaeaceae

Dais cotinifolia L.—Stem produces fiber.

Gnidia glauca (Fresen.) Gilg.—Stem produces best fiber for ropes.

G. latifolia (Oliv.) Gilg. Modide (Boni), Mwata (Swahili).—Shredded bark is used as thread.

G. subcordata Meisner. Lokilisiai (Dorobo).—Bark produces fiber for making baskets.

Peddiea fischeri Engl. (syn. *P. volkensii* Gilg.). Mucinjigiri (Kikuyu).—The bark produces fiber.

Struthiola thomsonii Oliv.—The bark produces fiber for making baskets.

Tiliaceae

Corchorus olitorius L.—A very good fiber is obtained from the bark.

Glyphaea brevis (Spreng.) (syn. *G. lateriflora*). Mukoma-nyakabito (Lunyoro).—The bark yields a fiber used in western Uganda.

Grewia bicolor Juss.

G. forbesii Mast.

G. goetzeana K. Schum.

G. holstii Burret.

G. mollis Juss.—The above five species are all exploited for fiber used in finishing edges of wickerwork baskets.

G. tenax (Forssk.) Fiori.—Sticks used for construction of granaries in Karamoja.

G. trichocarpa A. Rich. Powo (Luo).—The bark yields a tie fiber used in building huts, granary and hut doors.

Triumfetta macrophylla K. Schum. var. *ruwenzoriensis* (Sprague) Sprague & Hutch. Mugio (Kikuyu), Mughambi (Luo), Ekinsambwe (Luganda).—The bast fiber is used in finishing edges of wickerwork baskets. Also used in making granaries.

T. pilosa Roth. Mukiswa (Kamba).—The bast fiber is used for baskets by the Akamba.

T. rhomboidea Jacq. Murindunguri (Kikuyu), Mulawa (Kamba), Luwugula (Luganda).—The bark fiber is used for finishing wickerwork winnowing baskets.

T. tomentosa Boj. Owichi (Luo), Ndizi (Taita), Mugio (Kikuyu), Ekinsambwe (Luganda).—The bast fiber used as in *T. macrophylla.*

Ulmaceae

Trema guineensis (Schum. & Thonn.) Ficalho.—The inner bark is used as rope and a reddish-brown dye is obtained from the bark.

Urticaceae

Obetia pinnatifida Bak. Ikhobe (Taita), Nokoret (Dorobo).—The stem fiber is used for rope by the Dorobo and for woven baskets by the Taita.

Pouzolzia hypoleuca Wedd.—Strong fiber obtained from inner bark is used for fishing nets.

Urera hypselodendron (A. Rich.) Wedd. Nyandetu (Kikuyu).—Bast fiber is used by the Kikuyu.

Verbenaceae

Avicennia marina (Forssk.) Veirh. Mchu (Swahili), Mtsari (Giriama).—A brown dye is obtained from pounded and mashed bark in water.

Clerodendrum acerbianum (Vis.) Benth. & Hook. f. Mkwembe (Giriama).—Wood fiber is used for fish traps.

Vitaceae

Cissus quadrangularis L. Sukurtuti (Dorobo).—The stem is used as a binding rope for granaries and doors.

C. rotundifolia Vahl. Minya (Luo), Lalaite (Dorobo).—Stems used as rope for ganaries and the shredded stem is used for filter at end of straw for drinking homemade beer.

Cyphostemma adenocaule (A. Rich.) Wild & Drum. Lodore (Kakwa), Mugangalungo (Giriama).—Stems used as string. A red dye is obtained from the roots and used to color twilled winnowing baskets by the Giriama.

Rhoicissus revoilii Planch. Bumwe (Luo).—The stems are used as rope or string in making granaries.

MONOCOTYLEDONS

Agavaceae

Draceana ellenbeckiana Engl. Muronguton (Pokot).—The leaves are used for traps and for panniers.

D. steudneri Engl.—Leaves are used by Kipsigis to make baskets.

Sansevieria spp.—Many species of *Sansevieria* are exploited for fiber from the leaves, which is used in various woven baskets. The following species are known to be used in East Africa.

S. conspicua N. E. Br. Makonjemala (Giriama), Ewok (Pokot).

S. dawei. Obugoigo (Ankole).

S. ehrenbergii Bak. Emojo (Turkana).

S. kirkii Bak.

S. powellii N. E. Br. Makonge (Swahili).

S. raffillii N. E. Br.

S. robusta N. E. Br. Sorokitwa (Pokot), Eima (Rendille), Barat (Karamoja).

Cyperaceae

Cyperus alternifolius L. Maria (Teita).—The culms are used in making covered carrying baskets.

C. articulatus L.—Culms used in basket work in Tanzania.

C. dives Del. Kangogo (Swahili).

C. immensus C. B. Cl.—The stems are woven together with *Triumfetta* fiber to make chicken brooder in western Kenya.

C. laevigatus L.—Stems are used in making traps and string belts.

C. maranguensis K. Schum. Siga (Shambaa).—Stem used in fine basket work in Tanzania.

C. papyrus L. Kitoogo (Luganda), Toogo (Luo).—Split stems are used for a number of articles—wickerwork pot stands, twilled bird decoy cages, winnowing tray, etc.—while the pith is used in finishing edges of fishing baskets.

Fimbristylis ferruginea (L.) Vahl. Serig (Somali).—Stems are used in making fruit baskets.

Mariscus luteus (Boeck.) C. B. Cl. Entaratare (Ankole).—The stems are used in plaited grass platters in western Uganda.

Rhynchospora corymbosa (L.) Britt. Minyi (Kihehe).—Split stems are used in basketry and matting in southern Tanzania.

Dioscoreaceae

Dioscorea asteriscus Burkill.—A brown dye is obtained by mashing leaves and stems in water.

Flagellariaceae

Flagellaria guineensis Schum. Mpewa (Swahili).—Stems are used for fish traps.

Gramineae

Arundinaria alpina K. Schum. Teichan (Endo, Pokot).—Split stems are used in various wickerwork baskets, the ones made by Endo and Pokot looking like a half gourd are used as plates or for cleaning grain. They are also used for doors and screens being joined by *Triumfetta* or *Hibiscus* fiber.

Cymbopogon sp., probably *C. caesius* (Hook & Arn.) Stapf. Amasinde (Luhya).—The leaves are woven twilled style but loosely to make a bird decoy.

Cynodon nlemfuensis Vanderyst. Modhno (Luo).—The long stolons are used for making fishing baskets in western Kenya as well as for small measuring baskets and small food bowls.

Echinochloa pyramidalis (Lam.) Hitchc. & Chase.—Split culms are used in making open wickerwork baskets.

Eleusine coracana (L.) Gaertn., the Finger millett. Obulo (Ankole), Wimbi (Kikuyu).—The shiny culms are split and used as the lapping strip in coiled type baskets. The fine baskets are usually used as food bowls.

E. indica (L.) Gaertn. ssp. *africana* (Kennedy-O'Byrne) S. M. Phillips.—The split stem used as in *E. coracana* in Tanzania.

Eragrostis olivacea K. Schum.—The culms are used as the core bundle in coiled type fine baskets.

Humbertochloa greenwayii C. E. Hubb. Mianzi Mdogo (Kizaramo).—Used for making platelike baskets.

Hyparrhenia rufa (Nees) Stapf.—A common thatch grass used in screens and large grain storage containers.

Imperata cylindrica (L.) P. Beauv. var. *africana* (Anderss.) E. C. Hubb. Obiya (Luo), Lusenke (Luganda).—The leaves are split and made into local beer strainers. Also used in making fishing baskets.

Loudetia kagerensis (K. Schum.) Hutch. Buoywe (Luo).—The thin culms are used for bundle core in coiled type fine baskets.

Oxytenanthera abyssinica (A. Rich.) Munro.—The split stem is used in wickerwork basketry, making open or covered baskets.

Pennisetum purpureum Schumach.—Split stems are used to make wickerwork baby cots and ordinary open or covered baskets.

Phragmites mauritianus Kunth. Odundu (Luo), Amakada (Luyha).—The split reeds are used in wickerwork baby baskets (cots), flower baskets, storage baskets, and screens.

Saccharum spontaneum L.—The split culms are used for rough baskets.

Sporobolus agrostoides Chiov. Yweywe (Luo).—Used for fine baskets.

Liliaceae

Aloe wilsonii Reynolds.—The sap produces a dye.

Asparagus flagellaris (Kunth) Bak. (syn. *A. paulliguilelmi*). Ergek (Rendille), Ergeg (Somali), Lukalanganjoro (Kinyamwezi).—The roots produce string used in basketry.

Marantaceae

Marantochloa leucantha (K. Schum.) Milne-Redh. Njulu (Luganda).—Very important in making the coiled type fine baskets in Uganda, the split stem is dried and wetted before use as the lapping strip around a core bundle of dried strips of banana leaf midrib.

M. purpurea (Ridl.) Milne-Redh. Mawulugungu (Luganda).—Used in the same way as the above but producing coarser work.

Musaceae

Musa holstii K. Schum.—Leaf stalk used as fiber for traps.

M. paradisiaca L., the "plantain," and *M. sapientum* L., the cultivated banana.—The dried basal sheaths are used as fiber for tying and for making a number of articles including fruit and wastepaper baskets. The midrib is split dried and forms the core bundle for coiled type baskets.

Palmae

Borassus aethiopum Mart. Ntunku, Ntungo, Katugu (Luganda), Ekitugu (Lunyoro), Nyadokanet (Ateso).—The leaves are used for making mats and baskets, especially in Karamoja.

Elaeis guineensis Jacq. Mba (Kuamba).—This palm has many economic uses, and leaves produce fiber used in basketry.

Eremospatha haullevilleana De Wild. Enga (Luganda).—The leaflets are used for sewing back of beehives, and the split rhachis is used for twilled chair seats and backs.

Hyphaene spp.—Doum palms are very important in

the drier parts in Uganda, Tanzania, and Kenya, especially in the north and on the coast, where they are common. Various articles are made, including water-carrying or honey storage baskets made like pots and sealed with beeswax, panniers, and mats. The following Doum palms are used.

H. compressa H. Wendl. Mkoma (Swahili), Hedi (Boni), Mlala (Giriama), Kone (Boran), Bar (Somali).

H. coriacea Gaertn.—The young leaves are used in making water-carrying baskets by the Gabbra, Boni, and Turkana.

H. petersiana Mart. (syn. *H. ventricosa* Kirk.). Egoli (Turkana).—The leaves are used in making fishing baskets.

Phoenix reclinata Jacq. Mukindu (Luganda), Kiangachi (Teita), Oltukai (Masai).—The leaves are widely used for baskets, sleeping mats, and plaited bags in Turkana, Uganda, and Kenya coast.

Raphia farinifera (Gaertn.) Hylander (syn. *R. ruffia*). Mwaale (Swahili), Kibo (Luganda).—The fiber from young unexpanded leaf is used for wickerwork and for coiled baskets.

Smilacaceae

Smilax kraussiana Meissn.—Stems used for making basket work by Kenya Tea Company.

Typhaceae

Typha latifolia L. Ondhong (Luo).—The leaves are made into a basket for keeping salt.

Zingiberaceae

Curcuma domestica Val. (syn. *C. longa*).—A yellow dye is obtained from the tuber, and the leaves are used for plaiting work in Tanzania.

TRADITIONAL METHODS OF TREATING SKIN DISEASES IN KENYA THROUGH THE USE OF PLANTS[1]

J. O. Kokwaro[2]

Abstract

Kenya, like many other African countries, has a long history of traditional medicine which has been practiced for many years and continues to play a major role in primary health care. Before the arrival of European missionaries and explorers with their modern medicine, our ancestors lived in this country, and naturally they would fall sick or get injured at certain times. The largest human organ and the most susceptible to both diseases and physical attacks is the skin. This paper deals with the indigenous drug plants used in Kenya for the treatment of different skin diseases. Since not all skin diseases mentioned would always respond positively to traditional plant therapy, I apply the term "treatment" in a broader context and avoid the term "cure." A disease such as leprosy is known to the herbalists as difficult to cure. However, the various plants listed under this disease are those which have been used to treat it. A total of 117 species are dealt with in this paper.

Résumé

Le Kénya, comme beaucoup d'autres pays africains, a une longue histoire de médecine traditionnelle qui est pratiquée depuis de nombreuses années et continue à jouer un rôle important dans notre médecine de base. Avant l'arrivée des missionnaires et des explorateurs européens avec leur médecine moderne, il arrivait parfois à nos ancêtres de tomber malade ou de se blesser. Il n'y a pas de doute que le plus grand organe humain et celui qui est le plus susceptible de tomber malade ou d'être blessé physiquement est la peau. Je vais donc parler ici des plantes médicinales indigènes que les kenyans utilisent pour le traitement des différentes maladies de peau. Toutes les maladies mentionnées ne répondent pas toujours favorablement à une thérapie traditionnelle par les plantes, et j'utilise donc le terme 'traitement' dans un contexte plus large évitant ainsi le terme de 'guérison.' Les herboristes savent qu'il est difficile de guérir une maladie telle que la lèpre. Cependant, les diverses plantes énumerées pour cette maladie sont celles qui ont été utilisées pour la traiter. L'auteur examine un total de 117 espèces dans cet article.

The skin (cutis) has the following layers: horny layer (stratum corneum), clear layer (stratum lucidum), granular layer (stratum germinativum), and basal-cell layer (stratum basale). The last two layers comprise the germinative zone and all the layers collectively form the epidermis. The skin is the largest organ of the body and, apart from being the protective cover of the body surface, it acts as a regulator of body temperature, controls excessive loss of water as well as organic and inorganic materials, and synthesizes several important substances used in the body. The outer cells of the skin are constantly shed. Below the epidermis is a tough, flexible and elastic layer called the dermis which contains many blood vessels and is thicker than the epidermis. There are a variety of pigments in the skin, and skin color is largely due to the presence of melanin and carotene.

There are many kinds of diseases affecting the skin. The following terms are used in this report: skin bleeding (dermatorrhagia), blistering (epispastic, vesigatory), deficiency of pigment (albinism, alphosis, leucopathia), disease (dermatosis, dermatopathy), dryness (xeroderma), inflammation (dermatitis, dermitis), pain (dermalgia, dermatalgia), and many others. Following closely the classification of skin diseases outlined in chapter 10 of the *Medicinal Plants of East Africa* (Kokwaro, 1976), I include some recent information I have gathered relating to specific diseases. Ectoparasitic diseases and wounds caused by snakebite are not included in this discussion. The vernacular names following each scientific name are from the tribes who supplied the information.

Four major groups of skin diseases are covered in a tabular form as follows: A. Wounds (including sores and ulcers); B. Dermatitis, itches and rashes; C. Leprosy; D. Ringworms. Each section has a brief description of the disease concerned and is followed by a table giving the bo-

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tanical and local names of the plant used, part of the plant used, the preparation of the plant drug, and how it is dispensed.

A. *Wounds* (including sores and ulcers). A wound is a breach in the continuity of body tissue and is usually accompanied with bleeding due to the rupture of blood vessels. Most plants used in traditional medicine against wounds are of certain balsams and resins to stop bleeding and help the wound heal. Other plants used for this purpose have astringent (binding) properties possibly due to the presence of such compounds as tannin. Both wounds and bleeding have a wide range of plant remedies. The list (Table 1) is retricted largely to the dicotyledons used in this purpose.

B. *Dermatitis, itches, and rashes.* Dermatitis is broadly inflammation of the skin and can be of many types. Itch is a common symptom of many skin conditions and refers to a peculiar irritating sensation in the skin. Rash is a lay term used for any skin eruption but more commonly for acute inflammatory dermatoses. Rashes and dermatitis due to allergic or other causes are frequently treated with antihistamines which suppress histamine release. Most antihistamines also relieve pruritus (itching). A traditional remedy for itches is similarly used for rashes and other kinds of dermatitis. Drugs for traditional treatment of these diseases are often mixed with oil or fat, notably ghee. This gives it both anti-inflammatory and cooling effects.

C. *Leprosy.* Leprosy is a chronic disease primarily affecting the nerves and skin but also other organs. It is caused by *Mycobacterium leprae.* There are two major types: tuberculoid leprosy, mainly affecting the skin and nerves, and lepromatous leprosy. Both types can occur in four forms, depending on the individual resistance or tissue response to the bacilli: indeterminate, tuberculoid, borderline, and lepromatous.

D. *Ringworm.* This is a fungal infection of the skin and its appendages. Infection may be caused by a number of genera of fungi of the class *Hyphomycetes.* Some may only affect the skin (e.g., *Malassezia furfur* and *Cladosporum werneckii*) whereas others affect the hair (e.g., *Piedraia hortai* and *Trichosporon beigelii*). Cutaneous mycoses involving the hair and skin are produced by species of *Microsporum* and *Trichophyton,* and this group includes various types of ringworm. The traditional treatment of the most common type of ringworm which affects children is done by first shaving the head and thereafter applying a prescribed herbal medicine.

Conclusions

The lore of the herbalist is unquestionably the treasure of Black Africans as a whole, a patrimony which we as modern scientists should preserve, propagate, and improve on at all costs. We are currently experiencing the rapid disappearance of genuine traditional herbalists and a decline of authentic knowledge in traditional medicine. It is therefore for the modern Kenyan biologists, chemists, and doctors to find out the active principles contained in these plants and suggest how best such compounds can be made into modern medicines. In fact, these are the kinds of research which are giving the American and European scientists new discoveries in modern antibiotics and drugs.

Literature Cited

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TABLE 1. Plants recorded in Kenya for treatment of skin diseases. Native tribe in parentheses, using the following abbreviations: Bor. = Borana; Dor. = Dorobo; Gir. = Giriama; Kik. = Kikuyu; Kips. = Kipsigis; Mar. = Marakwet; Mas. = Masai; Nan. = Nandi; Seb. = Sebei; Som. = Somali; Swa. = Swahili; Tai. = Taita; Tur. = Turkana.

Botanical Name	Native/Trade Name	Part Used	Preparation/Comment
	A. WOUNDS, SORES, AND ULCERS		
Acanthaceae			
Justicia striata	Kipkalamion (Mar.)	Whole plant	Crushed and juice used, or burnt and ash applied.
Apocynaceae			
Tabernaemontana holstii	Kibombo (Digo)	Latex	Latex from leaves or stems applied directly onto the wound.
T. usambarensis	Kitondo (Luhya)	Latex	As above.
Asclepiadaceae			
Huernia keniensis	Kawala (Kamba)	Sap	Sap from crushed stems used.
Periploca linearifolia	Sinidet (Mar.)	Latex	Latex from crushed stem. Contains glucoside periplocin.
Stapelia semota	Kawala (Kamba)	Sap	Whole plant crushed and the sap used.
Bignoniaceae			
Kigelia africana	Masina, Mvongonia, (Tai.), Muratina (Kik.), Rotio (Mar.), Yago (Luo)	Fruit	Juice from crushed fruit contains tannin.
Boraginaceae			
Ehretia cymosa	Murembu (Meru), Shekutu (Luhya)	Leaves	Infusion of crushed leaves.
Trichodesma zeylanicum	Nyalak-dede (Luo)	Leaves	Infusion of crushed leaves.
Burseraceae			
Commiphora africana	Mbambara (Swa.), Mutungu (Kamba), Tola	Sap	Gum resin from crushed leaves or bark.
Capparaceae			
Cadaba farinosa	Eren (Tur.), Mvunyavumo (Swa.)	Leaves	Pounded dry leaves used.
Capparis cartilaginea	Chepteretwa (Mar.)	Roots	Juice from crushed roots contains sulphur oil.
Maerua triphylla	Chokotwa (Pokot), Lito (Dor.), Ol-oiresoi (Mas.), Mulingula (Kamba), Mlala-mbuzi (Swa.)	Roots	Root infusion used.
Combretaceae			
Combretum molle	Eguyen (Tur.), Kembel (Seb.), Keyo (Luo), Kiama (Kamba), Mwama (Tai.), Olmororoi (Mas.)	Leaves	Used in place of cotton to cover the drug before finally using the dry banana pseudostem as a bandage.
Compositae			
Ageratum conyzoides	Ilusa (Luhya), Kundambara (Swa.), Oluoro-Chieng (Luo)	Leaves	Crushed and soaked in water or pounded and applied direct. Very popular with the Luo as a haemostatic.

TABLE 1. Continued.

Botanical Name	Native/Trade Name	Part Used	Preparation/Comment
Aspilia mossambicensis	Lilelie (Luhya), Mutanzi (Digo), Muti (Kamba), Raywetigo	Leaves	Pounded and applied.
Crassocephalum crepidioides	Lifululwa (Luhya)	Leaves	Pounded and juice squeezed onto the wound.
Galinsoga parviflora	Jepkondewa (Mar.), Mnyenye (Meru)	Stems and leaves	Pounded and juice squeezed onto the wound.
Gutenbergia fischeri	Ol-makirikirieny (Mas.)	Leaves	Crushed and applied.
Gynura valeriana	Imbuni (Luhya)	Leaves and flowers	Powder from leaves or flowers applied.
Notonia sp.	Ini-la-ng'ombe (Digo)	Leaves	Pounded and juice applied.
Senecio lyratipartitus	Rwinkithia (Meru)	Roots	Dried, pounded, and the powder applied.
Vernonia aemulans	Fuka (Digo)	Leaves	Dried and burnt and the ash rubbed on fresh wounds. Digo women use this to cure fresh cuts made on their abdomen as decoration. *Vernonia* have alkaloids.
V. karaguensis	Muya (Luo), Navimuli (Luhya)	Leaves	Boiled and the decoction used for washing the wound.
V. lasiopus	Muatha (Meru), Muhasha (Swa.), Muvatha (Kamba)	Leaves	Pounded and the paste put on the wound.
V. wakefieldii	Kiluma-ng'ondi (Tai.)	Bark	Crushed and applied.
Crassulaceae			
Kalanchoë densiflora	Kuserwet (Kips.), Kavila-mbodza (Gir.)	Leaves	The succulent leaves are heated and the juice squeezed onto the wound.
Euphorbiaceae			
Acalypha racemosa	Mwadzaji (Digo)	Leaves	Burnt and ash used.
A. villicaulis		Leaves	Soaked or boiled and the infusion used for washing the wound.
Croton macrostachyus	Musutsu (Luhya), Mutundu (Kamba, Kik.), Mutuntu (Meru)	Leaves	Crushed, soaked in water, and the juice used.
Euphorbia grantii	Muthuri (Meru)	Branches, stem	Latex applied onto the wound to stop bleeding and as a cure.
E. hirta	Muziyaziya (Digo), Mwache (Swa.)	Branches, leaves	The wound is covered with fresh leaves.
E. inequilatera	Lokile (Tur.)	Branches, stem	Powder from dried and pounded parts used.
Hymenocardia acida	Okango (Luo)	Bark	Dried and pounded into powdery form.
Jatropha curcas	Mbogo-komo (Gir.)	Latex	Fresh latex from leaves or stem used.
J. nogalensis	Jilba-dig (Som.)	Latex	Used as above.
Synadenium grantii	Fangafa, Ofangafa (Luo)	Latex	Fresh latex from leaves and stems applied on fresh decoration marks cut on the surface of women's abdomen. The healing is accomplished with a little swelling, which is the decoration.

TABLE 1. Continued.

Botanical Name	Native/Trade Name	Part Used	Preparation/Comment
Ricinus communis	Castor oil plant (Trade), Libono (Luhya), Mbono (Swa.), Mbonu (Tai.), Odagwa (Luo)	Leaves	Young leaves crushed and applied to the wound.
Labiatae			
Hoslundia opposita	Mdahamwita (Swa.), Mutserere (Digo, Gir.), Ofwong'o (Luo), Omufwofwo or Shikuma (Luhya)	Leaves	Crushed, soaked in water, and applied.
Plectranthus sylvestris	Muoro (Meru), Nginga (Tai.)	Leaves	Crushed and the juice squeezed onto the wound.
Satureja abyssinica	Kamungala (Kamba)	Whole plant	Decoction used for bathing by circumcised boys.
Lauraceae			
Ocotea usambarensis	Kivumba, Manyolo (Tai.), E. African camphorwood (Trade), Muura (Meru), Muzaiti (Kik.)	Bark	Pounded and the powder used for dressing wounds.
Leguminosae			
Acacia polyacantha	Falcon's claw acacia (Trade), Mkengewa (Banjun, Swa.)	Leaves	Dried, pounded, mixed with oil and applied.
Dalbergia melanoxylon	Mwengo (Meru)	Bark	Decoction used for cleaning wounds.
Dichrostachys cinerea	Dunguu (Tai.), Etirai (Tur.), Jirime (Bor.), Mkingiri (Swa.), Msativu (Boni), Mundua (Kamba), Okiro (Luo)	Bark	Pounded and applied.
Erythrina abyssinica	Mjafari (Swa.), Gorggorwa (Mar.), Murembe (Luhya, Luo), Muuti (Meru)	Bark	Burnt and ash used.
Indigofera arrecta	Sarkelat (Mar.)	Leaves	Crushed and juice used.
Leucaena leucocephala	Munyaa (Digo)	Roots	Burnt and the ash called "Kago" (Digo) rubbed onto cuts.
Malvaceae			
Abutilon fruticosum	Bolambal (Som.)	Roots	Dried and pounded or burnt and ash applied.
Sida ovata	Uvyaio (Kamba)	Bark	Dried, pounded, and applied.
Menispermaceae			
Cissampelos pareira	Libugu (Digo)	Roots and leaves	Burnt and the ash applied.
Monimiaceae			
Xymalos monospora	Mwawusungu (Tai.)	Leaves, roots	Dried and pounded into a powdery form, applied.
Ochnaceae			
Brackenridgea zanguebarica	Mchonga Mahana (Digo)	Roots	Dried and pounded into a yellow powder.

TABLE 1. Continued.

Botanical Name	Native/Trade Name	Part Used	Preparation/Comment
Ochna mossambicensis	Muchu, Mpamapama (Digo)	Bark	Crushed and the paste applied.
Oleaceae			
Olea hochstetteri	Elgon Olive (Trade), Musharagi (Kik.), Murguiwet (Nan.), Olloliondo (Mas.)	Bark	Brunt and the ash applied.
Pedaliaceae			
Josephinia africana	Comudu (Boni)	Roots	Pounded into powdery form, mixed with sheep's fat, and used for dressing the wound.
Polygalaceae			
Securidaca longipedunculata	Mzigi (Digo, Swa.)	Roots	Dried and pounded.
Polygonaceae			
Rumex abyssinica	Kinyonywe (Kamba)	Roots	Dried and pounded.
Heinsia crinita	Mvunja-jembe (Digo)	Leaves, roots	Burnt and ash used.
Salvadoraceae			
Salvadora persica	Ethokoni (Tur.), Kizungumoto (Tai.), Muezamoyo (Digo), Oremit (Mas.)	Bark	Crushed and juice used.
Scrophulariaceae			
Rhamphicarpa herzfeldiana	Chepneskut (Kips.), Esegi-ekop (Mas.)	Leaves	Crushed or pounded and juice squeezed on wound to stop bleeding.
Simaroubaceae			
Brucea antidysenterica	Kingame (Kamba)	Leaves	Pounded and mixed with ghee.
Solanaceae			
Solanum incanum	Sodom apple (Trade), Mtunguja (Swa.) and many vernacular names	Fruits	For fresh wound, break the fruit and apply the juice. Contains alkaloid solanine and is believed to be antibacterial.
S. nigrum	Ndulu (Kamba), Osuga (Luo)	Leaves	Pounded, soaked in water, and the infusion used.
Withania somnifera	Kipkogai (Mar.), Muanzo (Kamba)	Leaves	Burnt and the ash used; contains alkaloids.
Tiliaceae			
Grewia occidentalis	Muherogendi (Meru), Murundu-rundu (Kik.)	Bark	Juice squeezed out and applied to the wound.
G. similis	Aroya (Luo), Chomisiat (Dor.), Ekeli (Tur.), Mutuva (Kamba), Olneligwe (Mas.)	Bark	As above. Both species contain tannin mucilage.
Triumfetta rhomboidea	Lohandi (Luhya), Miungu-moto (Digo), Tumone (Boni)	Roots	Crushed and juice squeezed onto the circumcision wound.
Verbenaceae			
Lippia javanica	Ang'we-rao (Luo), Muri-	Leaves	Pounded and applied.

TABLE 1. Continued.

Botanical Name	Native/Trade Name	Part Used	Preparation/Comment
	thi (Kamba), Ol-Sinoi (Mas.), Sulasula (Luhya)		
Vitaceae			
Cissus quadrangularis	Macheso (Digo)	Stem	The fiber from the stem used.
Rhoicissus revoilii	Mtambaa-dume (Swa.)	Stem, roots	Dried, pounded and the powdery form used, or crushed and juice squeezed onto the wound.
R. tridentata	Durutua (Luhya)	Stem	Crushed and the juice squeezed onto the wound.
	B. DERMATITIS, ITCHES, AND RASHES		
Acanthaceae			
Crabbea velutina	Jumao (Som.), Kitab-cheptarbus (Mar.)	Whole plant	Dried, pounded and mixed with some oil.
Amaranthaceae			
Psilotrichum scleranthum	Chibiriti, Mkibiriti (Digo)	Leaves	As above.
Asclepiadaceae			
Pergularia daemia	Kipche (Mar.)	Leaves	Crushed and juice applied.
Bignoniaceae			
Spathodea campanulata	Flame of the forest, Nandi flame (Trade), and many local names	Bark	Decoction used for bathing babies with rashes.
Compositae			
Aspilia pluriseta	Muti (Kamba), Ol-oiya-basa (Mas.)	Leaves	Pounded and the paste rubbed on the infected part.
Crassocephalum mannii	Tergekwa (Mar.)	Leaves	Decoction used for washing the body.
Sphaeranthus kirkii	Chipepo, Mupepo (Digo), Kivrumbani (Swa.)	Whole plant	As above.
Euphorbiaceae			
Croton macrostachyus	Musutsu (Luhya), Mutundu (Kamba, Kik.), Mutuntu (Meru)	Bark and roots	Decoction used for bathing babies with rashes.
Labiatae			
Ajuga remota	Chebonyirar (Mar.), Mataliha (Luhya)	Leaves	Pounded and juice rubbed on the infected part.
Leguminosae			
Acacia brevispica	Kiptare (Mar.), Mughobari (Luhya), Ol-girigiri (Mas.)	Roots	Decoction for bathing. Contains mucilage and tannin.
Albizia gummifera	Mughonzulu (Luhya), Seet (Kips., Mar.)	Roots	Pounded roots soaked in water for bathing. Contains kosotoxin.
Erythrina abyssinica	Kivuti (Kamba), Mjafari (Swa.), Murembe (Luhya, Luo), Ol-goroshe (Mas.)	Bark	Burnt and ash used.

TABLE 1. Continued.

Botanical Name	Native/Trade Name	Part Used	Preparation/Comment
Meliaceae			
Ekebergia rueppelliana	Korbut (Mar.)	Bark	Decoction used for bathing, contains tannin.
Myricaceae			
Myrica salicifolia	Kitaloswa (Mar.)	Leaves	Pounded, mixed with ghee, and rubbed on the infection.
Myrsinaceae			
Maesa lanceolata	Kalatera (Luo), Lisebe-sebe (Luhya), Mborio (Mar.)	Bark	Decoction used for washing the infection, contains the glucocide embelic acid.
Oleaceae			
Olea africana	Wild Olive (Trade), Mutamaiyu (Kik.), Tamiyai (Samb.), Ol-orien (Mas.), Yemit (Kamas, Mar., Seb.)	Bark	Decoction used for bathing and drinking.
Podocarpaceae			
Podocarpus gracilior	Podo (Trade), Benet (Kamas, Elgeyo, Mar.), Musengera (Kik.)	Bark	As above.
Polygalaceae			
Polygala erioptera	Agwonyo (Luo)	Whole plant	Crushed, mixed with ghee, and rubbed on the rashes.
Polygonaceae			
Polygonum salicifolium	Burika (Luhya)	Leaves	Crushed, mixed with a little water, and rubbed on the infection.
Proteaceae			
Faurea saligna	Mosambonet (Nan.), Bwonget (Elgeyo), Sirirte (Mar.)	Bark	Decoction used for bathing and drinking.
Rubiaceae			
Spermacoce princeae	Gakungathe (Kik.), Murkugwet (Kips.), Omotakiebo (Gusii)	Whole plant	Pounded, mixed with ghee, and rubbed on the infection.
Sapindaceae			
Cadiospermum halicacabum	Binyna (Luo)	Leaves and roots	As above.
Sapotaceae			
Manilkara sulcata	Kurag (Boni), Mkuraki (Bajun)	Leaves and roots	Pounded and the paste rubbed on the infection.
Solanaceae			
Solanum incanum	Sodom apple (Trade) and many local names	Fruits	Cut the fruit and apply the content. Contains the alkaloid solanine.
Withania somnifera	Kipkogai (Mar.), Mwanzo (Kamba)	Fruits	Cut the fruit and apply the content.

TABLE 1. Continued.

Botanical Name	Native/Trade Name	Part Used	Preparation/Comment
Vitaceae			
Cyphostemma cyphopetalum	Kiptora (Mar.)	Leaves	Crushed and the paste applied on the infection.
	C. LEPROSY		
Amaranthaceae			
Cyathula cylindrica	Ng'atunyat (Kips.)	Whole plant (including roots)	Boiled and the decoction drunk and used for bathing.
Asclepiadaceae			
Calotropis procera	Boah (Som.), Etithuru (Tur.), Mpamba-mwi-tu (Swa.)	Bark and roots	As above.
Boraginaceae			
Cordia ovalis	Sandpaper tree (Trade), Msasa (Swa.), Muthia (Kamba), Mukuo (Meru, Kik.), Ol-seki (Mas.), Oseno (Luo)	Leaves and roots	The patient is exposed to a steam bath of the decoction, the body is then washed with the decoction, and a pounded paste of the bark rubbed on the infections.
Combretaceae			
Combretum apiculatum	Kiama (Kamba)	Roots	Decoction drunk for the treatment of the disease during its initial stages.
C. molle	Eguyen (Tur.), Kembel (Seb.), Keyo (Luo), Kiama (Kamba), Mwama (Tai.), Ol-mororoi (Mas.)	Roots	Decoction drunk.
Euphorbiaceae			
Acalypha ornata		Roots	Decoction drunk 2–3 times a day, and also used for bathing.
Simaroubaceae			
Brucea antidysenterica	Kingame (Kamba)	Leaves	Pounded, mixed with ghee, and rubbed.
Vitaceae			
Ampelocissus africana	Munwamadzi (Gir.)	Roots	Decoction drunk and some used for bathing.
	D. RINGWORM		
Chenopodiaceae			
Chenopodium album *C. opulifolium* *C. pumilio*	Nyatigotigo (Luo)	Leaves	Pounded, mixed with oil, and the paste smeared on the infection. For head infection, the hair is cut short to the scalp before the drug is applied. Contains some oil like ascanidole and can be very effective.

TABLE 1. Continued.

Botanical Name	Native/Trade Name	Part Used	Preparation/Comment
Compositae			
Aspilia mossambicensis	Lilelia (Luhya), Muhepe (Digo), Muti (Kamba), Raywetigo (Luo)	Leaves, fruits	Pounded and rubbed on the infection.
Leguminosae			
Cassia didymobotrya	Ithaa (Kamba), Lubino (Luhya), Kilao (Meru), Mshua (Tai.), Mwenu (Kik.), Omovenyu (Gusii), Owinu (Luo), Ol-senetoi (Mas.), Senetwet (Kips.), Mar (Nan.)	Leaves	Pounded, mixed with oil, and the paste smeared on the infection. Or burnt, ash mixed with oil, and smeared on the infection. The hair is cut short before the application of the drug.
Melastomataceae			
Dissotis senegambiensis	Manyas-olele (Luo)	Leaves	Pounded and the paste rubbed on the infection. Note the vernacular name *manyas* = medicine for, *olele* = ringworm.
Oxalidaceae			
Oxalis corniculata	Awayo (Luo)	Whole plant	Pounded, mixed with ghee, and the paste smeared on the infection. Contains oxalic acid in the form of acid potassium oxalate.
Sapindaceae			
Allophylus abyssinicus	Lusasari (Luhya)	Roots	Crushed, mixed with salt and oil, and rubbed.
Cardiospermum grandiflorum	Burili (Luhya)	Leaves	Pounded and the paste rubbed on the infection.
Solanaceae			
Datura stramonium	Barutu, Chemongong' (Kips.), Mwalola (Tai.), Silulu (Luhya)	Leaves and seeds	Dry, grind, mix with ghee, and smear on the infection. The plant is poisonous and contains alkaloids hyoscine, hyoscyamine, and atropine.
Solanum incanum	Sodom apple (Trade), Mtunguja (Swa.), and many vernacular names	Fruit	Cut or break the fruit and smear the juice on the infection. Widely used and believed to be effective. Contains alkaloid solanin and is probably both antibacterial and antifungal.

CONTRIBUTION À LA CONNAISSANCE DES PLANTES MÉDICINALES DES TURUMBU DE LA ZONE DE BASOKO (ZAIRE)

M. A. Mandango et M. B. Bandole[1]

Résumé

Cinquante-huit plantes médicinales sont actuellement recensées à Basoko chez les Turumbu. Elles sont utilisées principalement dans le traitement de maladies telles que notamment: affection de la cornée de l'oeil, annexite, bronchite, carie dentaire, diarrhée, folie, hémorroïdes, malformation lombaire, mycose, myométrie, neuropaludisme, othalgie, rougeole, etc. Parmi ces plantes, dans la région de Kisangani, *Ageratum conyzoides, Boerhaavia diffusa,* et *Musa paradisiaca* ont des effets antibiotiques sur le développement de *Staphylococcus aureus,* et *Cassia alata* et *Myrianthus arboreus* sont des plantes fébrifuges et antimalariques. De plus, parmi 72 espèces connues comme des plantes antiblennoragiques et antisyphilitiques nous en avons reconnu sept qui guérissent d'autres maladies chez les Turumbu à Basoko: *Bridelia atroviridis, Maesopsis eminii, Sida rhombifolia, Similax kraussiana, Ricinodendron heudelotii, Cassia alata,* et *Harungana madagascariensis,* ces trois dernières sont reconnues comme plantes antilépreuses. En dehors du territoire étudié deux de nos plantes possèdent des propriétés antivénériennes: *Boerhaavia diffusa* et *Piper guineense.* Ce premier inventaire montre l'existence de certaines plantes qui peuvent être utilisées dans le traitement de plusieurs maladies différentes, par example *Bridelia atroviridis* contre la blennoragie, la syphylis et la carie dentaire; *Cassia alata* pour guérir la lèpre, la malaria et la mycose; *Boerhaavia diffusa* protège contre l'empoisonnement et combat les maladies vénériennes; *Harungana madagascariensis* lutte contre l'anémie et guérit la lèpre; *Maesopsis eminii* est utilisé contre les maladies vénériennes, l'annexite et la myométrie; *Myrianthus arboreus* est employé efficacement contre la malaria et l'empoisonnement et *Ricinodendron heudelotii* guérit la lèpre et combat la folie. Une étude exhaustive fera ressortir surement l'abondance des plantes ayant un très large spectre d'action médicinale dans nos régions africaines.

Abstract

Fifty-eight medicinal plants have been recorded to date from the Turumbu tribe at Basoko. They are used principally in treating problems of the cornea of the eye, bronchitis, dental decay, diarrhea, insanity, hemorrhoids, lumbar malformations, mycosis, myopia, neuromalaria, othalgia, measles, etc. Among these plants, in the region of Kisangani, *Ageratum conyzoides, Boerhaavia diffusa,* and *Musa paradisiaca* have antibiotic effects against the development of *Staphylococcus aureus,* and *Cassia alata* and *Myrianthus arboreus* are febrifugous and antimalarial. Among the 72 species known to be antigonorrheal and antisyphilitic, seven have been found to be used in treating other diseases by the Turumbu: *Bridelia atroviridis, Maesopsis eminii, Sida rhombifolia, Smilax kraussiana, Ricinodendron heudelotii, Cassia alata,* and *Harungana madagascariensis,* the latter three known to be antileprous. Outside of the study area two of our plants possess antivenereal properties: *Boerhaavia diffusa* and *Piper guineense.* This first inventory shows certain plants that could be used in treating several different diseases, e.g., *Bridelia atroviridis* against gonorrhea, syphilis, and dental decay; *Cassia alata* for healing leprosy, malaria, and mycosis; *Boerhaavia diffusa* protects against poisoning and combats veneral disease; *Harungana madagascariensis* is useful in treating anemia and cures leprosy; *Maesopsis eminii* is used for veneral diseases, annexitis, and myopia; *Myrianthus arboreus* is used effectively against malaria and poisoning; and *Ricinodendron heudelotii* cures leprosy and combats insanity. An exhaustive study would surely reveal additional plants with a large spectrun of medicinal activity in our African region.

La zone administrative de Basoko est située à l'ouest dans la Région du Haut-Zaïre dont le chef-lieu est Kisangani: 0°30'N, 25°10'E et altitude ±420 m (Szafranski & Apema, 1983). Elle appartient à la zone bioclimatique des forêts ombrophiles équatoriales. La température moyenne annuelle généralement élevée oscille autour de 25°C. Les précipitations atmosphériques sont abondantes et assez bien réparties toute l'année, et leur moyenne annuelle est supérieure à 1.500

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mm par an. En ce qui concerne l'humidité relative de l'air, la station climatologique de Lokutu indique une valeur moyenne annuelle de 84%.

Occupation Humaine

D'après Baptist (1951), le véritable nom des Turumbu serait Likile qu'ils rattacheraient tantôt à un ancêtre éponime, tantôt au cri d'un petit singe très répandu dans leurs forêts. Turumbu serait alors un sobriquet qui signifierait "gens de l'intérieur de la forêt" par opposition aux "gens de l'eau," les riverains. De la Likati les Turumbu se seraient dirigés vers le sud où ils auraient peuplé la rive droite du fleuve Zaïre.

Nous ne disposons d'aucun document récent qui puisse donner le nombre de populations Turumbu. Actuellement elles sont réparties en plusieurs cheferies hétérogènes plus ou moins concentrées à Barumbu, Basoko, Isangi, Yangambi, Yanonge, Yambaw, Yawemda, et Weko. Ces différentes fractions de population parlent des dialectes apparentés dont les plus connus sont Kingelema, Lehanga, et Likile.

Les Turumbu pratiquent l'agriculture intinérante. Cependant ils s'intéressent de plus en plus de la pêche comme leurs viosins les Lokele sur le fleuve Zaïre et ses principaux affluents.

Présentation du Sujet

Au Zaïre De Wildeman (1935) figure parmi les premiers à récenser les plantes médicinales, et à Kisangani Bokdam & Droogers (1975) ont présenté une première étude éthnobotanique des Wagenia. Les plantes médicinales des environs de Kisangani sont bien connues (Wome, 1982, 1984a, 1984b).

Cet article est une contribution à la connaissance des plantes médicinales du Zaïre. Il présente les premiers résultats de nos recherches éthnobotaniques de 1981 à 1983 chez les Turumbu de la zone de Basoko dans le Haut-Zaïre.

Matériel et Méthodes

Nos investigations sur le terrain ont été réalisées au cours des années 1981–1983. Nous avons ainsi récolté un matériel d'herbier et constitué un herbier de référence dont une partie est conservée à l'herbarium de la Faculté des Sciences de l'Université de Kisangani. Une autre partie est déposée dans la collection de plantes forestières de la section des Eaux et Forêts à l'Institut Supérieur d'Etudes Agronomiques de Bengamisa.

Nous avons utilisé deux méthodes classiques pour la réalisation de notre étude:

Enquête éthnobotanique. Pour obtenir des renseignements sur les noms vernaculaires des plantes, et les modes de préparation et d'administration des médicaments, nous avons procédé par un questionnaire préalablement établi. Ce questionnaire a été posé à plusieurs personnes âgées réputées "guérisseurs" ou praticiens. Leur âge au-dessus de 50 ans pouvait être déduit des rides de leur visage.

Étude bibliographique. Elle a consisté à compulser d'abord les données antérieures locales disponibles sur le sujet et ensuite des ouvrages sur les plantes médicinales recensées ailleurs en Afrique. Les résultats de ce travail de compulsion, de vérification, et de comparaison ont complété les renseignements personnels issues de nos enquêtes. En ce qui concerne la distribution phytogéographique de plantes inventoriées nous nous sommes inspirés de la chorologie des plantes vasculaires de la Tshopo établie par Lejoly & Lisowski (1978).

Pour la plupart des plantes recensées et reprises à la liste floristique, les noms vernaculaires sont ajoutés à la suite du nom des taxons en indiquant entre parenthèses l'abrégé de dialecte auquel ils appartiennent. Nous avons (LE) pour Lehanga, (LI) pour Likile, et (LO) pour Lokele (Tableau 1).

Par ailleurs, dans la phytothérapie combinée le guérisseur ou le praticien fait intervenir dans la préparation de ses remèdes divers ingrédients tels que notamment des cailloux altérés par la foudre (CF), de la terre provenant d'une termitière construite en étage (TE), des débris végétaux charriés par le fleuve ou autre cours d'eau (DF), de la terre issue de la termitière-nid des tortues (TT), et des matières organiques humifiées (MH) épaisses sur laquelle se développent certains champignons comestibles de couleur brune du genre *Prinus*.

Dans la zone étudiée des observations cliniques approfondies sont recommandées dans le diagnostic exact de folie et de neuropaludisme. Dans les deux cas les symptômes se caractérisent par un délire angoissant et un monologue criard, insensé, quelque fois injurieux agaçant tout l'entourage. Dans la région, seul le guérisseur perçoit les distinctions symptômatologiques entre les deux maladies dans leur phytothérapie.

TABLEAU 1. Plantes médicinales des Turumbu de la zone de Basoko.

Noms scientifiques	Noms vernaculaires	Chorologie[a]
Acanthaceae		
Asystasia vogeliana Benth.	–	GC
Barleria opaca (Vahl) Nees	Makoko motobi (LE) Makoko moa tombi (LI)	GC
Thomandersia hensii De Wild. et Th. Durand	Bokoka (LE) Litindi (LI)	CGC
Annonaceae		
Polyalthia suaveolens Engl. et Diels	Imbai (LE)	CGC
Apocynaceae		
Baissea axillaris (Benth.) Hua	Asini na lobe (LE)	CGC
Araceae		
Anchomanes giganteus Engl.	Ligboma mbula (LE) Ligboma mbula (LI)	Zaï
Pistia stratiotes L.	Losongele (LO)	Pan
Asteraceae		
Ageratum conyzoides L.		Pan
Spilanthes filicaulis (Schum. et Thonn.) C. Adams		GC
Synedrella nodiflora Gaertn.	Lifoloto kolo (LE) Lifolotokolo (LI)	GC
Vernonia conferta Benth.	Lihihi loa meme (LE) Likumba (LI)	Pan
Caesalpiniaceae		
Cassia alata L.	Litunda loa kolo (LE) Boumba nana (LI)	Pal
Pachyelasma tessmannii (Harms) Harms	Lindeko (LE) Lindeko (LI)	CGC
Combretaceae		
Combretum smeathmannii G. Don	Kolole (LE) Kolele (LI)	GC
Cyperaceae		
Scleria boivinii Steud.	Ngangatea (LE) Longangatea (LI)	Af-Mal
Euphorbiaceae		
Bridelia atroviridis Müll. Arg.	Bonduagu (LE) Botoku (LI)	At
Hymenocardia ulmoides Oliver	Botengelenge (LE) Litengelenge (LI)	At
Phyllanthus discoideus (Baillon) Müll. Arg.	Lekele (LE)	At
Ricinodendron heudelotii (Baillon) Pierre ex Heckel	Bohongo (LE) Losongo (LI)	GC
Tetrorchidium didymostemon (Baill.) Pax et K. Hoffm.	Molelileli (LE) Molelileli (LI)	GC
Fabaceae		
Mucuna flagellipes Vogel ex Benth.	Andosa (LE) Mokaso (LI)	GC
Pterocarpus soyauxii Taub.	Ibulu (LE)	CGC

TABLEAU 1. Continuer.

Noms scientifiques	Noms vernaculaires	Chorologie[a]
Hypericaceae		
Harungana madaga scariensis Lam. ex Poir.	Bondokbo (LE) Londokbo (LI)	Af-Mal
Icacinaceae		
Chlamydocarya thomsoniana Baillon	—	GC
Irvingiaceae		
Klainedoxa gabonensis Pierre ex Engl. var. *oblongifolia* Engl.	Bosuu (LE) Lisuu (LI)	CGC
Loganiaceae		
Strychnos icaja Baillon	Bohehe (LE)	GC
Loranthaceae		
Loranthus albiziae De Wild.	Ekbondakbonda (LE) Ekbondakbonda (LI)	CGC
Malvaceae		
Sida rhombifolia L.	Atiohole (LE) Atouhole (LI)	Pan
Mimosaceae		
Acacia pentagona (Schum.) Hook. f.	Ingbalala (LE) Lokonda (LI)	GC
Piptadeniastrum africanum (Hook. f.) Brenan	Akungu (LE)	GC
Moraceae		
Chlorophora excelsa (Welw.) Benth. et Hook. f.	Mokongo (LE) Mokongo (LI)	GC
Ficus exasperata Vahl	Lisosea (LE) Lohoha (LI)	At
Myrianthus arboreus P. Beauv.	Bokoo (LE) Botoke (LI)	GC
Musaceae		
Musa paradisiaca L.	Lebogo (LE) Liboo (LI)	Pan
Myristicaceae		
Pycnanthus angolensis (Welw.) Exell	Lifonde (LE) Lifonde (LI)	GC
Staudtia gabonensis Warb.	Monanga (LE) Monanga (LI)	CGC
Myrsinaceae		
Embellia pellucida K. Schum.	Ekongo (LE)	At
Nyctaginaceae		
Boerhaavia diffusa L.	Litindi loa mbongo (LE) Ambundambunda (LI)	Pan
Olacaceae		
Olax gambecola Baillon	Sasabikila (LE) Epianda aa pü (LI)	GC
Pandanaceae		
Microdesmis puberula Hook. f.	Bokeleketea (LE) Ikelekete (LI)	GC

TABLEAU 1. Continuer.

Noms scientifiques	Noms vernaculaires	Chorologie[a]
Piperaceae		
Piper guineense Schum. et Thonn.	Keleketu (LE) Ketsu (LI)	GC
Piper umbellatum L.	Libondobondo (LE) Liondondo (LI)	Pan
Poaceae		
Streptogyna crinita P. Beauv.	Itoakengo (LE) Ngeangea (LI)	Pal
Rhamnaceae		
Maesopsis eminii Engl.	Mongangalanga (LE) Mongangalanga (LI)	GC
Rubiaceae		
Mussaenda elegans Schum. et Thonn.	Atoko atoko (LE) Atoko atoko (LI)	GC
Pseudomussaenda stenocarpa (Hiern) Petit	Basapongo (LE) Atoko atoko (LI)	CGC
Sapotaceae		
Autranella congolensis (De Wild.) A. Chev.	Lepanga (LE)	CGC
Gambeya lacourtiana (De Wild.) Aubrév. et Pellegrin	Bokomba (LI)	CGC
Selaginellaceae		
Selaginella myosurus (Sw.) Alston	Eangambula (LI)	GC
Smilacaceae		
Smilax kraussiana Meisn.	Ingbakba (LE) Likalolo (LI)	At
Solanaceae		
Capsicum annuum L.	Mokakondo wahihü (LE) Ibasi üsunguisungu ((LI)	Pan
Nicotiana tabacum L.	Tumbako (LE) Tumbako (LI)	Pan
Urticaceae		
Urera hypselodendron (Hochst.) Wedd.	Fufulu ya hihü (LE)	At
Verbenaceae		
Vitex ferruginea Schum. et Thonn.	Botindikela (LE)	GC
Vitaceae		
Cissus adenopoda Sprague	Iyese (LI)	GC
Zingiberaceae		
Costus lucanusianus Braun-Blanquet	Ikagago (LE) Mokakado (LI)	GC
Renealmia africana (K. Schum.) Benth.	Lingasa laa lohe (LI)	CGC
Lichen		
Usnea sp.	Tua ta mondili (LE) Soe ya mondili (LI)	

[a] GC = espèce guinéo-congolaise, CGC = espèce centro-guinéo-congolaise, Zaï = espèce endémique zaïroise, At = espèce afrotropicale, Af-Mal = espèce afromalgache, Pan = espèce pantropicale, Pal = espèce paléotropicale.

Resultats

analyse floristique

Le premier inventaire des plantes médicinales des Turumbu de la zone de Basoko actuellement connu montre un total de 57 espèces comprenant 46 genres répartis dans 36 familles (Tableau 1). Nous comptons 35 familles des phanérogames avec 56 espèces et une famille des ptéridophytes avec une espèce. En plus, il convient de signaler également la présence d'un lichen du genre *Usnea* dont l'espèce n'est pas déterminée.

En ce qui concerne la distribution phytogéographique des espèces recensées, nous observons un gros lot de 37 espèces forestières soit 64,9% du total de la florule appartenant à la région guinéo-congolaise (White, 1979). A côté de ces espèces on note la présence de neuf espèces pantropicales soit 15,7% de l'ensemble spécifique. Les autres espèces sont moins bien représentées. Il s'agit notamment de sept espèces afrotropicales, deux espèces afro-malgaches et deux espèces paléotropicales intervenant respectivement pour 12,2%, 3,6%, et 3,6% de la florule de notre dition.

plantes utilisées et maladies traitées

Traitement simple

Il s'agit de combattre les premiers symptômes de la maladie ou de soigner les maladies encore peu graves. Dans tous les cas le guérisseur ou le praticien utilise une seule plante dans l'administration de remèdes.

Acacia pentagone. Empoisonnement: les jeunes feuilles froissées sont consommées par le personne empoisonnée qui expulse le poison par vomissement.

Ageratum conyzoides. Bronchite: les feuilles pilées et mélangées à l'eau donnent un liquide qui après filtration est bu à l'aide de cuillérée à soupe.

Anchomanes giganteus. Complication de l'accouchement: la macération dans l'eau des racines broyées intervient en lavement chez la parturiante.

Asystasia vogeliana. Folie, empoisonnement: l'infusion des feuilles est employée en boisson contre l'accès de folie ou contre l'empoisonnement.

Autranella congolensis. Folie: l'incinération de l'écorce de tige ou de racine est appliquée sur les scarifications faites sur le front.

Baissea axillaris. Folie: quelques gouttes de suc dérivant du broyat des racines sont instillées dans les yeux.

Barleria opaca. Folie, neuropaludisme et malformation lombaire: les feuilles sont préparées et consommées comme légume.

Boerhaavia diffusa. Prévention contre l'empoisonnement: les feuilles sont préparées et consommées comme légume.

Bridelia atroviridis. Carie dentaire: la macération de l'écorce de tige ou de racine dans l'eau tiède est employée pour laver abondamment la bouche.

Capsicum annuum. Affection de la cornée de l'oeil: quelques gouttes de suc provenant des feuilles frossées et par pressage sont instillées dans les yeux.

Cassia alata. Mycose: les feuilles sont pilées et frottées sur les parties malades de la peau. La décoction des feuilles est employée en lavement, après filtration.

Chlamydocarya thomsoniana. Prévention contre l'empoisonnement par boisson: une ou plusieurs feuilles sont mangées crues avant d'aller boire. Un vomissement accuse la présence d'un poison dans la boisson consommée.

Chlorophora excelsa. Folie, neuropaludisme et malformation lombaire: les feuilles sont préparées et consommées comme légume.

Cissus ademopoda. Courbature: l'infusion des feuilles est employée en lavement, après filtration.

Combretum smeathmannii. Folie: les cendres provenant de l'incinération de l'écorce de tige sont appliquées sur les scarifications faites sur le front. Malformation lombaire: la poudre issue de l'incinération de la tige est appliquée sur les scarifications effectuées sur les parties malades.

Costus lucanusianus. Annexite, myométrie et endométrie: le suc extrait des tiges par broyage est employé en lavement.

Embellia pellucida. Folie: l'écorce de racine pilée et mélangée à l'eau donne un liquide qui, après filtration, est instillée en gouttes nasales plusieurs fois par jour.

Ficus exasperata. Malformation lombaire: la décoction de l'écorce de tige est administrée en lavement après filtration.

Gambeya lacourtiana. Othalgie: le liquide tiède de la macération de l'écorce de racine est instillé dans l'oreille malade après filtration.

Harungana madagascariensis. Anémie: l'in-

fusion des feuilles est administrée en lavement après refroidissement. Ou encore, le suc extrait des feuilles par froissement et pressage est instillé dans les yeux.

Hymenocardia ulmoides. Prévention contre l'empoisonnement: les feuilles sont préparées et consommées comme légume.

Klainedoxa gabonensis var. *oblongifolia.* Abcès, furoncle: le fruit débarrassé de son épicarpe broyé avec de la chaux est appliqué sur la partie infectée.

Loranthus albiziae. Diarrhée: les cendres issues de la carbonisation de tige mélangée avec du sel de cuisine sont léchées par le malade.

Maesopsis eminii. Annexite, myométrie: l'écorce des racines pilée et mélangée à l'eau donne un liquide qui est employé en lavement après filtration.

Microdesmis puberula. Abcès, furoncle: les feuilles trempées dans l'huile de palme sont chauffées et frictionnées sur la partie infectée.

Mucuna flagellipes. Menace d'avortement: les feuilles pilées et mélangées à l'eau interviennent en lavement après filtration.

Musa paradisiaca. Entorse, déchirure des muscles et fracture: les jeunes tiges sont utilisés après un chauffement léger pour frictionner les parties souffrantes.

Mussaenda elegans. Folie: les fleurs, les feuilles et de la chaux sont pilées. Le produit est appliqué sur tout le corps du malade.

Myrianthus arboreus. Empoissonnement: les feuilles sont pilées et consommées crues par la personne empoisonnée.

Nicotiana tabacum. Carie dentaire: la poudre des feuilles séchées mélangée au kaolin est introduite dans la dent malade.

Olax gambecola. Neuropaludisme, empoisonnement: la macération de l'écorce de racines dans l'eau est administrée au malade sous forme de boisson en demi-verre tous les deux jours.

Pachyelasma tessmannii. Folie: les cendres provenant de la carbonisation de l'écorce de tige ou de racine sont appliquées sur les scarifications pratiquées sur le front.

Phyllanthus discoideus. Malformation lombaire: l'écorce de tige pilée et mélangée à l'eau donne un liquide qui est administrée en lavement, après filtration.

Piper guineense. Empoisonnement: les feuilles sont pilées, préparées et consommées par le malade.

Piper umbellatum. Malformation lombaire: la moelle est pilée en mélange avec de la chaux et du sel de cuisine. Le produit est appliqué sur les scarifications effectuées sur le dos.

Piptadeniastrum africanum. Folie: les cendres issues de la carbonisation de l'écorce de tige ou de racine sont appliquées sur les scarifications faites sur le front du malade.

Pistia stratiotes. Bronchite: l'eau dans laquelle sont pilées les feuilles est administrée au malade sous forme de boisson à l'aide de cuillérée à soupe.

Polyalthia suaveolens. Folie: les cendres provenant de l'incinération de tige ou de racine sont utilisées sur les scarifications effectuées sur le front du malade.

Pseudomussaenda stenocarpa. Neuropaludisme: le suc extrait de l'écorce de racine est instillé dans les narines du malade. Prévention contre l'empoisonnement: les jeunes feuilles sont mangées crues avant d'aller boire. Le vomissement après la consommation des feuilles accuse une boisson empoisonnée.

Pterocarpus soyauxii. Hémorroïdes: l'infusion de l'écorce de tige ou de racine est administrée en lavement après filtration.

Pycnanthus angolensis. Prévention contre l'empoisonnement: les feuilles sont préparées avec des oeufs et de l'huile de palme, puis consommées comme légume.

Renealmia africana. Neuropaludisme: les cendres provenant de l'incinération de tige sont appliquées sur les scarifications pratiquées sur le front du malade.

Ricinodendron heudelotii. Folie, neuropaludisme et malformation lombaire: les feuilles sont préparées et consommées indistinctement comme légume pour les trois cas.

Scleria boivinii. Neuropaludisme: la poudre issue de la carbonisation de tige est employée sur les scarifications faites sur le front du malade.

Selagiinella myosurus. Affection de cornée de l'oeil: la vapeur provenant des fragments de la plante chauffés est soufflée en direction de l'oeil malade.

Sida rhombifolia. Entorse, déchirure des muscles, fracture: les cendres provenant de la carbonisation de tige et de racine sont appliquées sur les scarifications pratiquées sur l'avant-bras du praticien ou du guérisseur. Celui-ci, de son avant-bras scarifié frictionne les parties souffrantes du patient. Plaie; la poudre

issue de l'incinération des feuilles est répandue sur la plaie ou encore elle est mélangée avec de l'huile de palme légèrement chauffée puis appliquée sur la plaie.

Smilax kraussiana. Annexite, myométrie: la macération dans l'eau des racines pilées intervient en lavement après filtration.

Spilanthes filicaulis. Carie dentaire: les feuilles sont pilées et introduites dans la galerie de la dent malade. Hernie: le suc extrait des feuilles pilées est administré en lavement après filtration.

Staudtia gabonensis. Carence de lactation: les feuilles bouillies sont utilisées pour masser les seins de la nourrice.

Streptogyna crinita. Neuropaludisme: la poudre provenant de l'incinération des tiges intervient sur les scarifications pratiquées sur le front du malade.

Strychnos icaja. Folie, neuropaludisme et malformation lombaire: les cendres résultant de la carbonisation des tiges ou des racines sont appliquées sur les scarifications faites sur le front (folie et neuropaludisme) et sur la partie malade (malformation lombaire).

Synedrella nodiflora. Othalgie: les feuilles finement froissées sont utilisées pour obstruer l'oreille malade.

Tetrorchidium didymostemon. Rougeole: l'écorce de tige ou de racine pilée et mélangée à l'eau est administrée en lavement après filtration. L'écorce pilée est également utilisée pour frictionner tout le corps.

Thomandersia hensii. Affection de la cornée de l'oeil: quelques gouttes de suc extrait des feuilles par froissement et pressage sont instillées dans l'oeil malade.

Urera hypselodendron. Malformation lombaire: la moelle pilée est appliquée sur les scarifications pratiquées sur la partie malade.

Usnea sp. Folie, neuropaludisme et malformation lombaire: la poudre noire est appliquée sur les scarifications effectuées sur le front (folie et neuropaludisme) et sur la partie malade (malformation lombaire).

Vernonia conferta. Malformation lombaire: la moelle mélangée avec de la chaux et du sel de cuisine est appliquée sur les scarifications pratiquées sur la partie malade.

Vitex ferruginea. Folie: les cendres résultant de la carbonisation de l'écorce de tige ou de racine sont appliquées sur les scarifications faites sur le front du malade.

Traitement combiné

Le guérisseur traite les cas de maladies graves en trois étapes au moins. Il associe dans chaque étape deux ou plusieurs plantes différentes dans la préparation de ses remèdes. Cependant, il convient de signaler le cas de rhumatisme articulaire aigu soigné par une seule plante.

Traitement de folie. 1ère étape. *Embellia pellucida*: la macération des racines broyées dans l'eau est instillée plusieurs fois dans les narines jusqu'à ½ verre par jour. *Baissea axillaris*: la macération des racines broyées dans l'eau est instillée, après filtration, dans les yeux deux fois par jour, matin et soir. *Asystasia vogeliana*: la décoction des feuilles est prise en boisson tous les deux jours. Le vomissement qui s'ensuit est un bon signe de guérison. *Mussaenda elegans*: les fleurs et les feuilles sont pilées en mélange avec de la chaux. Le produit est appliqué sur tout le corps du malade qui ne pourra se laver qu'après trois jours.

2ème étape. *Autranella congolensis, Combretum smeathmannii, Pachyelasma tessmannii, Piptadeniastrum africanum, Polyalthia suaveolens, Strychnos icaja, Usnea,* et *Vitex ferruginea*: la carbonisation des écorces des autres plantes et celle de tige de *Strychnos icaja* sont mélangées avec MH. On ajoute à la poudre obtenue des DF, de la TT, *Usnea* et du carbonate de soude (cf. page 374). Le produit est appliqué sur les scarifications faites à la base du nez, autour de la tête, derrière à la base du cou, en bas du sternum et sur les articulations de bras et de jambes.

3ème étape. *Barleria opaca, Chlorophora excelsa* et *Ricinodendron heudelotii*: les feuilles sont préparées comme légume avec de l'huile de palme, du sel de cuisine, du kaolin et des ndakala (poisson du genre *Stolothrissa*). Ce repas appelé kboto est donné en ultime remède pour signifier le fin de traitement.

Traitement de neuropaludisme. 1ère étape. *Pseudomussaenda stenocarpa*: la mácération des racines triturés est instillée dans les narines après filtration. Le patient devenu sourd et muet est interpelé par le guérisseur jusqu'à entendre et dialoguer avec ce dernier.

2ème étape. *Olax gambecola*: la décoction des racines est prise en boisson par le malade à la dose de ½ verre tous les deux jours.

3ème étape. *Barleria opaca, Seleria boivinii, Chlorophora excelsa, Renealmia africana, Ricinodendron heudelotii, Streptogyna crinita, Strychnos icaja,* et *Usnea*: on ajoute la poudre

d'*Usnea* et du carbonate de soude aux cendres issues de la carbonisation des tiges. Le produit est appliqué sur les scarifications faites à la base du nez, autour de la tête, derrière à la base du cou, en bas du sternum, et sur les articulations de bras et de jambes.

4ème étape. Les feuilles sont préparées comme légume avec de l'huile de palme, du sel de cuisine, du kaolin et des ndakala. Ce repas appelé kboto est donné en ultime remède pour signifier la fin de traitement.

Traitement de malformation lombaire et thoracique. 1ère étape. *Piper umbellatum, Urera hypselodendron, Usnea,* et *Vernonia conferta*: la moelle et de la chaux sont pilées en mélange avec des CF (cf. page 374). On y ajoute de la poudre d'*Usnea* et du carbonate de soude. Le produit est appliqué sur les scarifications pratiquées en V renversé sur le dos (entre les omoplates), à la base de sternum, derrière le cou, sur les épaules et sur les articulations de bras et de jambes.

2ème étape. *Combretum smeathmannii, Ficus exasperata, Phyllanthus discoideus, Piper umbellatum*: les tiges sont triturées en mélange avec des TT et déposées sur une feuille de *Piper umbellatum* que l'on charge dans un pot en argile. On y ajoute du copal qu'on allume aussitôt. Le pot chauffé est placé sur la tête du patient. Si la guérisson ne s'annonce pas, en prépare un mélange fait de carbonisation de tige de *Loranthus albiziae,* l'os frontal du crane de singe, de la poudre d'*Usnea* et du copal. Le produit est appliqué sur les scarifications pratiquées sur le sternum, sur les épaules et sur les articulations de bras et de jambes.

3ème étape. *Barleria opaca, Chlorophora excelsa,* et *Ricinodendron heudelotii*: les feuilles sont préparées comme légume avec de l'huile de palme, du sel de cuisine, du kaolin et des ndakala. Ce repas appelé kboto est donné en dernier remède pour signifier la fin du traitement.

Traitement de l'empoisonnement. 1ère étape. *Olax gambecola*: la macération des racines triturées est administrée après filtration, sous forme de boisson à la dose de ½ verre tous les deux jours. *Asystasia vogeliana*: l'infusion de feuilles est prise sous forme de boisson à la dose de ½ verre tous les deux jours. Un vomissement expulse le poison. L'une de deux plantes peut être utilisée si l'autre manque.

2ème étape. *Acacia pentagona, Myrianthus arboreus,* et *Piper guineense*: les feuilles sont préparées comme légume avec de l'huile de palme, du kaolin et du carbonate de soude.

Prévention contre l'empoisonnement. Boerhaavia diffusa, Hymenocardia ulmoides, et *Pycnanthus angolensis*: les feuilles tendres sont préparées avec de l'huile de palme comme légume auquel on ajoute un oeuf frais battu. Par la suite si on mange une nourriture empoisonnée un vomissement expulse le poison.

Traitement d'annexite et myométrie. 1ère étape. *Costus lucanusianus, Maesopsis eminii,* et *Smilax kraussiana*: la macération acqueuse des écorces de racine de *Maesopsis, Smilax* et des TE mélangée au suc extrait de tige de *Costus* donnent un liquide qui après filtration est administré en lavement deux fois par jour, matin et soir.

2ème étape. *Maesopsis eminii, Myrianthus arboreus,* et *Smilax kraussiana*: un morceau de souche d'arbre d'une piste et celui de tige de *Myrianthus* pris au niveau d'un noeud sont carbonisés en mélange avec l'écorce des racines de *Smilax* et *Maesopsis.* On y ajoute du carbonate de soude et le produit est appliqué sur les scarifications pratiquées transversalement sur le bas-ventre de la patiente.

Traitement d'abcès et de furoncle. Klainedoxa gabonensis var. *oblongifolia* et *Microdesmis puberula*: feuilles de *Microdesmis* trempées dans l'huile de palme et chauffées sur un feu doux sont utilisées en massage sur la partie infectée. La trituration de fruit de *Klainedoxa* en mélange avec de la chaux est frictionnée sur la partie douloureuse.

Traitement de l'affection de cornée de l'oeil. Selaginella myosurus: la vapeur provenant des fragments de la plante chauffées dans un cornet de feuille est soufflée en direction de l'oeil malade. *Thomandersia hensii*: le suc extrait des feuilles après froissement et pressage est instillé dans l'oeil (une ou deux gouttes) deux fois par jour, matin et soir. *Capsicum annuum*: le suc extrait des feuilles après froissement et pressage est instillé dans l'oeil (une ou deux gouttes) deux fois par jour, matin et soir. L'une de deux dernières plantes peut être utilisée si l'autre manque.

Traitement de carie dentaire. Spilanthes filicaulis et *Nicotiana tabacum*: les feuilles sont pilées et mélangées avec de la poudre de *Nicotiana tabacum.* Le produit est introduit dans la perforation de la dent malade (généralement une molaire).

Traitement de l'othalgie. Gambeya lacour-

tiana et *Synedrella nodiflora*: le suc extrait des racines de *Gambeya* est instillé dans l'oreille malade. En plus, les feuilles froissées de *Synedrella* sont utilisées pour obstruer l'oreille du malade dès le début du traitement.

Entorse, déchirure des muscles et fracture. Musa paradisiaca et *Sida rhombifolia*: le rejet de *Musa*, légèrement chauffé, est utilisé pour frictionner la partie souffrante. La poudre noire issue de carbonisation de racines et de tiges de *Sida* est appliqué sur les scarifications pratiquées sur l'avant-bras du guérisseur. Celui-ci de son avant-bras scarifié frictionne vigoureusement la partie souffrante du patient.

Rhumatisme articulaire aigu. Microdesmis puberula: on ajoute du carbonate de soude à la poudre résultant de la carbonisation de tige, une noix palmiste et une plume de perroquet. Le produit est employé sur les scarifications effectuées sur les parties douloureuses du patient.

Discussion et Conclusion

Cinquante-huit plantes médicinales sont actuellement recensées à Basoko chez les Turumbu. Elles sont utilisées principalement dans le traitement de maladies telles que notamment affection de cornée de l'oeil, annexite, bronchite, carie dentaire, diarrhée, folie, hémorroïdes, malformation lombaire, mycose, myométrie, neuropaludisme, othalgie, rougeole, etc.

Parmi ces plantes inventoriées dans notre dition Ndjele & Bigawa (1982) ont cité pour la région de Kisangani *Ageratum conyzoides, Boerhaavia diffusa,* et *Musa paradisiaca* ayant des effets antibiotiques sur le développement de *Staphylococcus aureus.* Dans la même région Wome (1982) a mentionné *Cassia alata* et *Myrianthus arboreus* comme plantes fébrifuges et antimalariques. De plus Wome (1984a) a inventorié 72 plantes antiblennoragiques et antisyphilitiques dont nous avons reconnu sept qui guérissent d'autres maladies chez les Turumbu à Basoko. Il s'agit des plantes suivantes signalées également dans certains pays africains: *Cassia alata* (Raponda-Walker & Sillans, 1961; Bouquet, 1969; Kerharo, 1971; Berhaut, 1971–1979), *Bridelia atroviridis* (Bouquet & Debray, 1974), *Harungana madagascariensis* (Staner & Boutique, 1937; Raponda-Walker & Sillans, 1961; Watt & Breyer-Brandwijk, 1962), *Maesopsis eminii* (Bouquet, 1969), *Ricinodendron heudelotii* (Raponda-Walker & Sillans, 1961; Watt & Breyer-Brandwijk, 1962; Bouquet, 1969), *Sida rhombifolia* (Staner & Boutique, 1937), et *Smilax kraussiana* (Staner & Boutique, 1937; Kerharo & Adam, 1974).

En dehors du territoire étudié deux de nos plantes possèdent des propriétés antivénériennes. Il s'agit de *Boerhaavia diffusa* in Staner & Boutique (1937), Robyns (1951), Bouquet (1969), Bouquet & Debray (1974) et *Piper guineense* cité par Robyns (1948), Raponda-Walker & Sillans (1961), Bouquet (1969), et Vergiat (1970).

En ce qui concerne les plantes antilépreuses de la région de Kisangani Wome (1984b) a cité *Ricinodendron heudelotii.* Par ailleurs sont reconnues également comme plantes antilépreuses *Cassia alata* d'après Staner & Boutique (1937), Watt & Breyer-Branwijk (1962), Adjanohoun & Aké Assi (1979), et *Harungana madagascariensis* cité par Staner & Boutique (1937), Bouquet (1969), et Bouquet & Debray (1974).

Ce premier inventaire montre l'existence de certaines plantes qui peuvent être utilisées dans le traitement de plusieurs maladies différentes. Nous citerons par exemple *Bridelia atroviridis* contre la blennoragie, la syphylis, et la carie dentaire; *Cassia alata* pour guérir la lèpre, la malaria, et la mycose; *Boerhaavia diffusa* protège contre l'empoisonnement et combat les maladies vénériennes; *Harungana madagascariensis* lutte contre l'anémie et guérit la lèpre; *Maesopsis eminii* est utilisé contre les maladies vénériennes, l'annexite, et la myométrie; *Myrianthus arboreus* est employé efficacement contre la malaria et l'empoisonnement; et *Ricinodendron heudelotii* guérit la lèpre et combat la folie.

Une étude exhaustive fera ressortir sûrement l'abondance des plantes ayant un très large spectre d'action médicinale dans nos régions africaines.

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CLIMATIC CORRELATES OF SPECIES RICHNESS FOR WOODY "EDIBLE" PLANTS ACROSS SOUTHERN AFRICA[1]

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ABSTRACT

About 20% of the woody plant species of southern Africa are known to be exploited as food resources by native peoples. Expecting that the distribution and diversity of edible wild plants would be subject to the same constraints influencing that of woody plants in general, a macro-level, first-order study was undertaken to: (1) map the geographic variation in species richness across this region, and (2) establish whether a predictable relationship exists between climate and geographic variations in the richness of edible plant species. The goal was to develop a model for predicting edible plant species richness as a function of climate—past, present, and future gradients of increasing richness. By using species distribution maps (264 species) and climate station data for southern Africa, it was possible to calculate and map the number of edible plants per unit area (grid richness), as well as ascertain the climatic parameters within a grid's area (ca. 150 km²). It was then possible to determine whether differences in grid richness could be statistically correlated to differences in grid climate. The results suggest that climate can be used to predict edible plant species richness; in particular, the minimum monthly potential evapotranspiration (PEMIN) and the maximum monthly precipitation (PMAX). When used together as a two-variable model, they explain 83% ($P < 0.0001$) of the variation. In effect, PEMIN and PMAX are interpreted to measure the photosynthetic capacity of the environment: length of growing season, and favorable heat, light, and moisture conditions. Geographic variations in species richness are interpreted to reflect the physiologic capabilities of these plants to adapt to differential accesses to the climatically-determined resources necessary for successful photosynthesis, growth, and reproduction in southern Africa.

RÉSUMÉ

On sait que les indigènes utilisent environ 20% des espèces ligneuses du sud de l'Afrique pour se nourrir. L'auteur, s'attendant à ce que la répartition et la diversité des plantes sauvages comestibles soient sujettes aux mêmes contraintes qui influencent celles des plantes ligneuses en général, a entrepris une étude à grande échelle afin de: 1) dresser la carte de la variation géographique dans la richesse des espèces à travers cette région, et 2) voir s'il existe une relation prévisible entre les variations climatiques et géographiques dans la richesse en espèces comestibles. Le but était de développer un modèle pour prédire la richesse en espèces comestibles comme une fonction du climat—gradients passés, présents, et futurs de richesse croissante. Il a été possible de calculer et de faire une carte du nombre de plantes comestibles par région aussi bien que d'établir les paramètres climatiques dans une région (ca. 150 km²). Pour ceci l'auteur a utilisé des cartes de répartition (264 espèces) et des données des stations météorologiques du sud de l'Afrique. Il fut alors possible de déterminer si des différences en richesse par région pouvaient être statistiquement reliées aux différences de climat. D'après les résultats il semblerait que le climat puisse être utilisé pour prévoir la richesse en espèces de plantes comestibles; en particulier l'évapotranspiration potentielle et mensuelle minimum (PEMIN) et la précipitation mensuelle maximum (PMAX). Quand on les utilise ensemble comme modèle à deux variables elles expliquent 83% ($P < 0{,}0001$) de la variation. En fait, PEMIN et PMAX sont interpretées comme mesurant la capacité photosynthétique de l'environnement: longueur de la saison de croissance et conditions favorables de chaleur, luminosité, et humidité. Selon l'auteur les variations géographiques dans la richesse en espèces reflètent les capacités physiologiques de ces plantes à s'adapter à des accès differentiels aux ressources déterminées par le climat nécessaires à une photosynthèse, une croissance, et une reproduction réussies dans le sud de l'Afrique.

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Traditional studies of southern Africa's wild plant foods focus on their macro- and/or micronutritional contributions to the native African diet, their medicinal properties, or their potential as future domesticates or famine foods (e.g., Fleuret, 1979; Lee, 1979; Newman, 1970; Scudder, 1962; Story, 1958, 1964; Williamson, 1976). Instead, I focused on the geography of these plants as a subset of the natural vegetation, primarily because of its importance to human ecology.

Throughout most of humankind's existence, the availability, diversity, and abundance of human plant food dietary resources were necessarily a function of the natural environment, directly influencing such human ecological parameters as seasonal subsistence and migratory behaviors, as well as population size and density (Peters & O'Brien, 1981). Today, technology—the supermarket, farm, and marketplace; domestication (plant and animal), greenhouses, and monoculture; processing, storage, and long-distance transport—increasingly circumvents the proclivities and whims of nature, allowing us to sustain huge populations and survive in otherwise uninhabitable areas. Yet wild edible plants continue to sustain us, particularly in the third world. Moreover, they are likely to sustain us tomorrow in the form of new plant domesticates and as the source of viable germplasm for use in genetic engineering (Duke, 1978). By understanding how the diversity of humanly edible wild plants changes across the landscape—which environments would be rich in dietary resources, which poor—we should gain a new perspective on human ecology, present and past. It might also prove useful in the planning and selection of environments for conservation purposes.

A review of the literature suggests that an investigation of geographic variations in species richness (a measure of diversity that considers only numbers of species but not their abundance, etc.) requires careful control of scale (Fischer, 1959) and size of grid (MacArthur, 1972) as well as use of environmental variables which enter into the ecosystem and relate well to diversity (Pianka, 1978). Like all terrestrial plant species, the presence or absence of humanly edible plants in a particular locale is most likely a function of natural history and their innate genotypic/phenotypic abilities to cope with and/or adapt to the restraints imposed by a given environment. Although soil, topography, and the biotic components of a given environment may be of importance (particularly at the meso- and microlevels of analysis), at a macrolevel of analysis the most important factor determining plant growth is suggested to be climate (Walter, 1979; Daubenmire, 1978; Whittaker, 1965, 1970). Considering the foregoing, the appropriate scale for the study of geographic patterns in species richness is that of macroscale (Fischer, 1959; Pielou, 1975). This is defined by Griffiths (1976) as an area greater than 100 km^2. The appropriate climatic factors in a study of species richness—given their direct relationship to photosynthesis—are suggested to be light, moisture, temperature, and how each of these factors fluctuates seasonally (Wulff, 1943; Griffiths, 1976; Pianka, 1966, 1978; Rohde, 1978; Baker, 1970; Pielou, 1975).

Expecting that the distribution and species richness of edible wild plants would be subject to the same constraints influencing that of plants in general, a first-order, macroscale study was undertaken to:

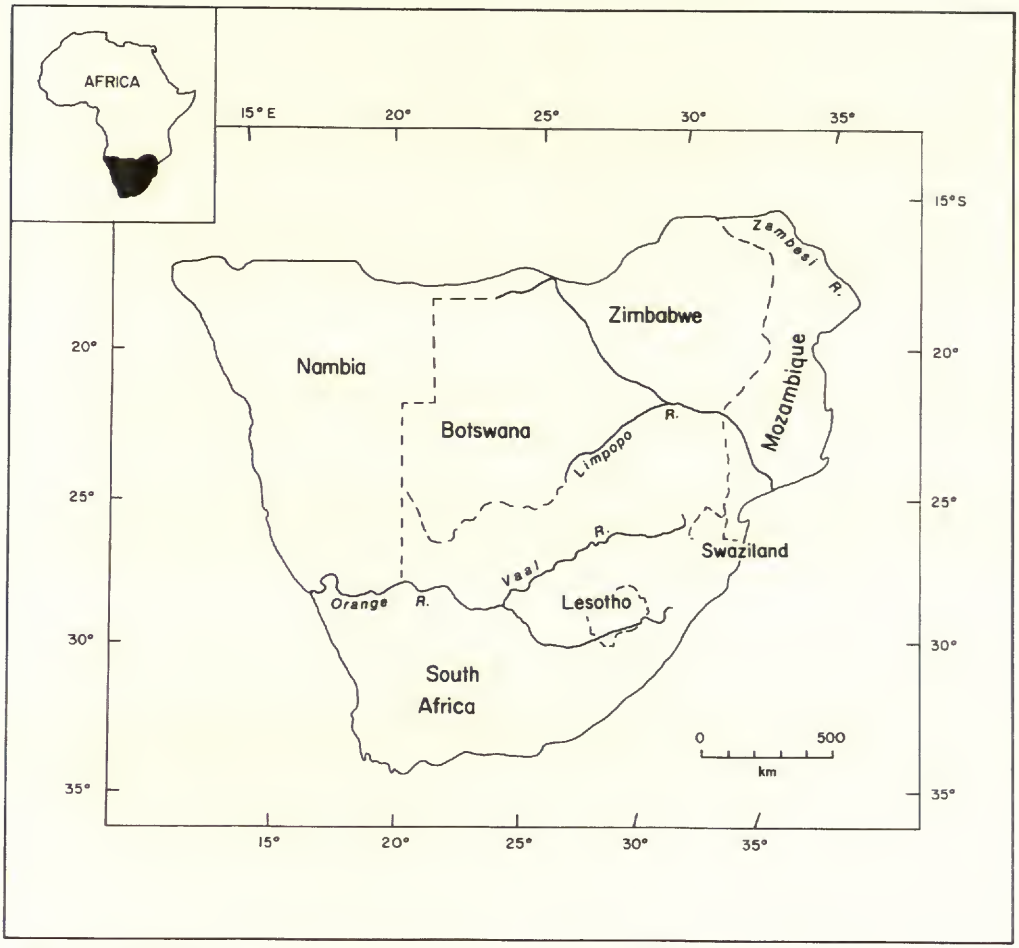
1. map the current geographic variation in the species richness of wild humanly edible plants; and,
2. establish whether a predictable relationship exists between climate and the observed geographic variations in the species richness of edible wild plants. Such a model should prove useful in generating qualitative maps of increasing potential species richness for areas outside the study area and for different times in the past, under different climatic regimes—discrete gradients of relative, but not absolute, potential species richness.

Following Fischer (1959), species range maps were used in conjunction with a macroscale grid system to map the geographic variation in species richness and to circumscribe both the species richness per grid and the climate data per grid so that the results could be statistically analyzed. At the time this study was undertaken, reasonably accurate species range maps existed only for the woody plants of southern Africa. The study was limited accordingly. Such a first-order approximation should set the stage for more detailed smaller-scaled studies. It may also contribute to a better understanding of plant species richness in general.

Materials and Methods

Study Area

Southern Africa is defined here as that part of continental Africa between 15°–34°S and 12°–41°E, an area encompassing almost 3,500,000



MAP 1. Study area.

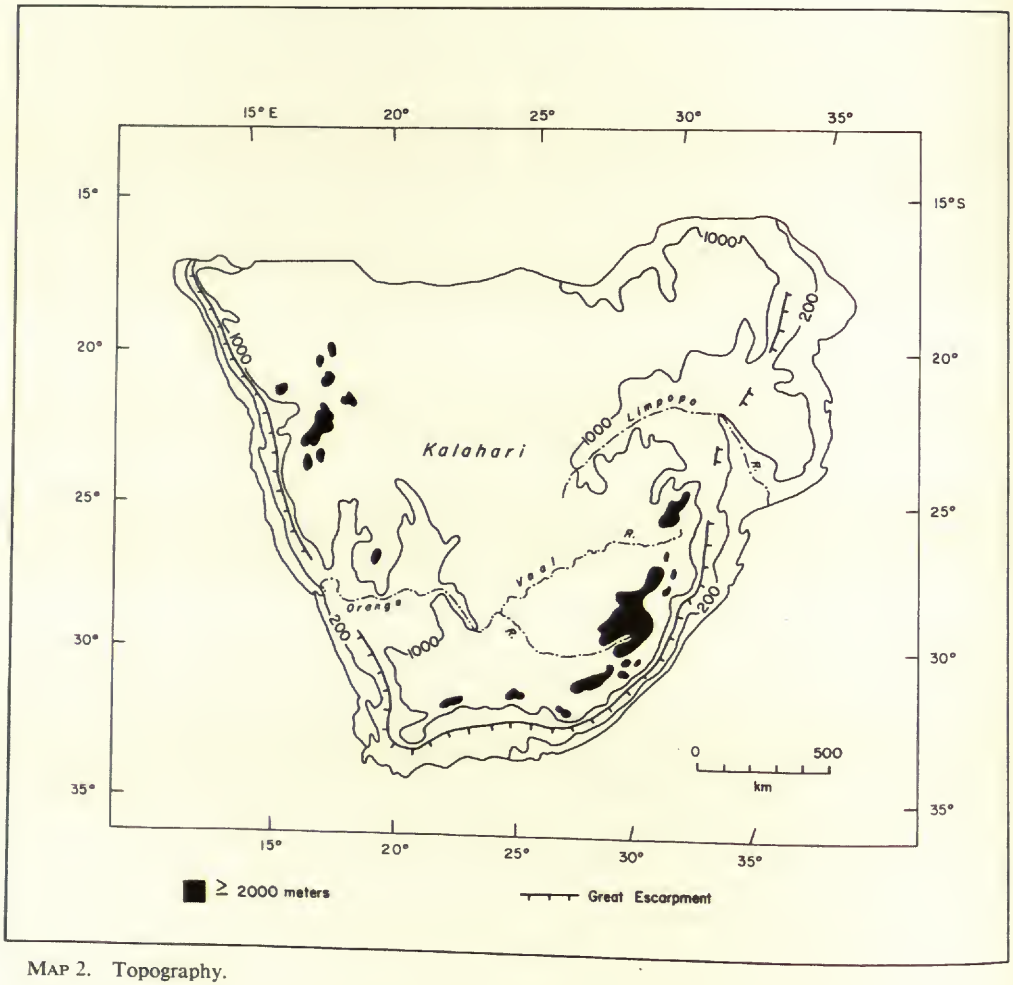
km² that is physiographically dominated by a bowl-shaped interior plateau (Maps 1, 2). It includes the countries of Namibia, Botswana, Zimbabwe, South Africa, Swaziland, Lesotho, and Mozambique south of the Zambezi.

MATERIALS

Edible woody plants are defined in this study as any woody plant that is exploited for food by humans in eastern and/or southern Africa. The plant parts consumed include roots, stems, shoots, leaves, bark, cambium, pith, fruits, berries, gums, flowers (including nectar), pods, beans, arils, and seeds. The woody plant types include deciduous, semievergreen, and evergreen bushes, shrubs, trees and lianes, as well as palmiforms and succulents.

The species range maps used in this study were taken from Palgrave's (1977) *Trees of Southern Africa*. A consensus of verbal opinions (from R. Drummond, Harare, and J. Anderson, Pretoria) suggested them to be accurate to within a radius of 40–80 km. With this in mind, the macroscale grid system utilized in this study divided southern Africa into equal-area units of 150 km on a side (22,500 km²). This scale was also consistent with the density of climate stations. By comparing Peters & O'Brien's (in prep.) *Survey of the Wild Edible Plants of Eastern and Southern Africa* with Palgrave's (1977) *Trees of Southern Africa*, it was possible to isolate edible species, calculate and map the number of species per grid, and, using latitude and longitude, assign climatic data to each grid.

The climatic data were taken from Thornthwaite & Mather (1962). This work was chosen



MAP 2. Topography.

primarily because of its more uniform data on potential evapotranspiration and actual evapotranspiration.

In a review of climatic indices and classification schemes used in the study of southern Africa's vegetation patterns and associations, Schulz & McGee (1977) found that the climatic variables most likely to discriminate the location and distribution of vegetation associations are those reflecting seasonal fluctuations in the duration and intensity of precipitation, temperature, and incoming solar radiation. Annual means of any of these factors were found to be less important by comparison. Both actual and potential evapotranspiration (as estimated using the Thornthwaite method) were found to be superior to temperature, either alone or in conjunction with some other variable. They further suggested that all these variables may be modified or regulated by the effects of latitude and elevation.

The climatic variables consequently used in this study reflect two major categories: energy and moisture (Table 1). Energy is represented by potential evapotranspiration (PE). Empirically derived, it is based on air temperature and day length. Expressed in millimeters, it measures the potential amount of water released into the atmosphere through both surface evaporation and the biological processes of respiration and transpiration. This is strongly dependent on temperature (Pianka, 1978); the greater the temperature, the greater the potential evapotranspiration. It is regulated as well by latitude, altitude, cloud cover, and slope (topography) (Pianka,

1978). The same factors, however, modify temperature. Theoretically, therefore, it is a measure of solar energy input and, conversely, the amount of water necessary to meet the evaporative demands at any given place (Griffiths, 1976; Mather, 1974, 1978).

Considering the foregoing, the independent energy variables used in the statistical analyses were: the minimum monthly potential evapotranspiration (PEMIN), the maximum monthly potential evapotranspiration (PEMAX), the range between these two extremes (DIFPE), as well as the annual value (PEAN).

The moisture category is represented primarily by precipitation (P), but also included here are actual evapotranspiration (AE) and Thornthwaite's Moisture Index (MI). Measured in millimeters, actual evapotranspiration is the amount of water actually released into the atmosphere through evaporation and the biological processes of respiration and transpiration. However, actual evapotranspiration is not a measure of climatic water demand as is potential evapotranspiration. Rather, it is real water loss and a function of vegetation type, soil type, soil moisture content, and land management practices, as well as climatic constraints (Mather, 1978). Actual evapotranspiration is considered to be equal to potential evapotranspiration whenever precipitation is greater than potential evapotranspiration, and equal to precipitation when potential evapotranspiration is greater than precipitation, plus the water removed from soil storage (Mather, 1978). In southern Africa, monthly actual evapotranspiration is virtually equal to monthly precipitation, except when and where monthly precipitation exceeds monthly potential evapotranspiration.

The Moisture Index (PMI) as defined by Thornthwaite & Mather (1962) is an estimate of the relative moistness or aridity of a climate. It is calculated using the expression

$$100[(P/PE) - 1]$$

(Thornthwaite & Mather, 1957, 1962; Mather, 1978) and measures how well the available moisture satisfies the climatic demands for water annually. It is a negative term in arid climates, positive in moist climates, and zero when precipitation is equal to potential evapotranspiration.

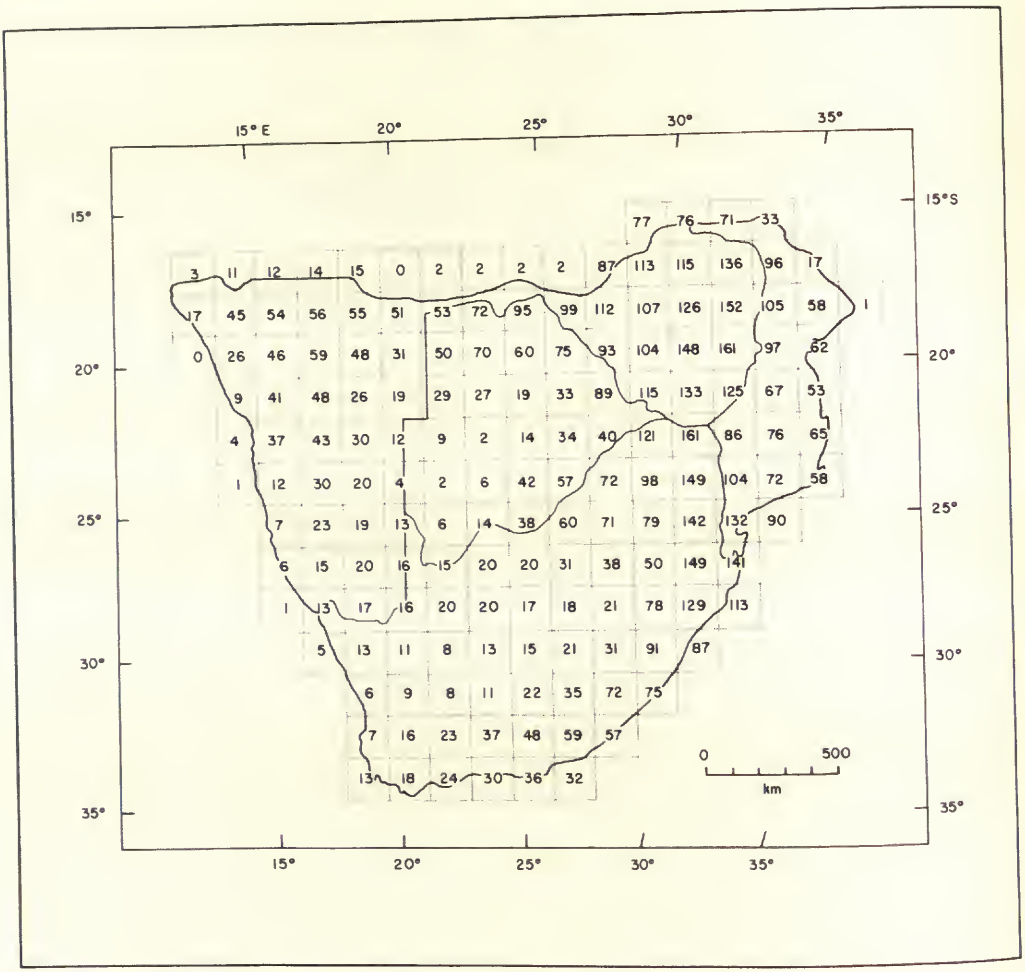
More generally, in semiarid areas such as southern Africa, water is often considered to be the "master" limiting factor (Pianka, 1978).

TABLE 1. Climatic variables (and symbols used in text).

Variable	Symbol	Unit of Measurement
Energy: Potential evapotranspiration	PE	mm
Annual PE	PEAN	mm/yr.
Maximum monthly PE	PEMAX	mm/mo.
Minimum monthly PE	PEMIN	mm/mo.
Range in monthly PE	DIFPE	mm/yr.
Moisture: Precipitation (rainfall)	P	mm
Annual P	PAN	mm/yr.
Average monthly P	PAVM	mm/mo.
Actual average monthly P	ACTP	mm/mo.
Maximum monthly P	PMAX	mm/mo.
Minimum monthly P	PMIN	mm/mo.
Range in monthly P	DIFP	mm/yr.
Precipitation in warmest month	PWARM	mm/mo.
Annual actual evapotranspiration	AE	mm/yr.
Moisture index	PMI	(ratio)

Odum (1969) found that in the absence of runoff a strong and positive linear correlation exists between rainfall and primary production. Furthermore, actual evapotranspiration has often been used as a global index of "biological activity." Net primary productivity has been found to be strongly correlated to annual actual evapotranspiration (Rosenzweig, 1968; Lieth & Box, 1972; Box, 1978) in environments ranging from barren deserts to rainforest, and Meentemeyer (1978) used actual evapotranspiration to estimate global patterns of litter decomposition rates. The Moisture Index is the cornerstone of the Thornthwaite classification system, which is in common use in southern Africa today.

Considering the foregoing, the independent moisture variables included in this study are: annual precipitation (PAN), annual actual evapotranspiration (AE), and Thornthwaite's Moisture Index (PMI). Seasonal fluctuations in moisture availability were represented by: minimum monthly precipitation (PMIN), maximum monthly precipitation (PMAX), the difference between these two extremes (DIFP), precipitation during the warmest month (PWARM), and average monthly precipitation (PAVM; defined as PAN/12). A special precipitation variable, ac-



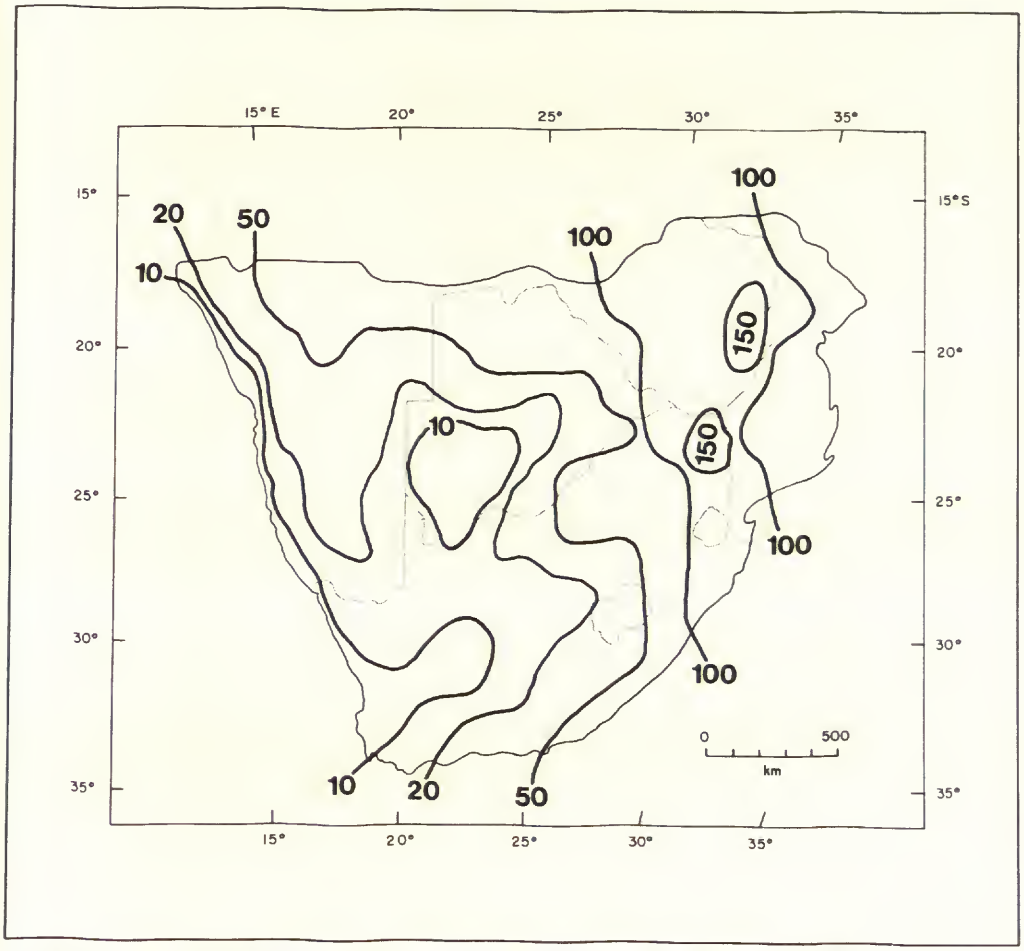
MAP 3. Geographic variation in species diversity across southern Africa.

tual average monthly precipitation during the rainy season (ACTP), was also included. It was calculated by dividing the number of months with precipitation greater than or equal to 10 mm into the amount of precipitation received during those months. For most of southern Africa, this is synonymous with the intensity of monthly precipitation during the growing season. Some form of plant dormancy (e.g., deciduousness) is not unusual in drought-susceptible areas or in areas with seasonally low temperatures. Lack of water during these months would not be as critical as lack of water during the potential growing season.

In addition to the energy and moisture variables discussed above, two secondary variables were also included: the number of months without drought stress (DROUGHT) and elevation (ELEVATION). Schulz & McGee (1977) used the number of months with precipitation ≤ 10 mm as a means of assessing drought stress within southern Africa. Conversely, this study used the number of months with precipitation ≥ 10 mm as a measure of the absence of drought stress, thus providing information on geographic variations in the maximum length of the growing season. Elevation, on the other hand, is the only aspect of topography considered statistically in this study. The elevation of the climate station, not the average for the grid area, was used. This is also reported in Thornthwaite & Mather (1962).

STATISTICAL ANALYSES

Statistical analyses were performed using SAS package programs (Helwig & Council, 1979): PROC UNIVARIATE for descriptive statistics



MAP 4. Isometric map of geographic variation in species diversity across southern Africa.

of each variable; PROC CORR to obtain the correlation coefficient matrix and significance tests for all the variables used in the study; PROC RSQUARE to determine the best single- and multiple-variable models for explaining the variation in geographic patterns of species richness across southern Africa; and PROC GLM to perform an analysis of variance and linear regression of the best single- and multiple-variable models explaining geographic patterns of species richness in southern Africa.

The criteria to be used in selecting the best single- and/or multiple-variable models are: that the variable(s) have a theoretically strong and sound relationship with species richness; that the variables be few in number to maintain parsimony; and high precision, e.g., a low mean square error (variance).

Only those grids with data on both species richness and climate were included in the statistical analyses. In addition, the following constraints were observed:

1. Since species richness is a function of the size of the area sampled, an attempt was made to keep the area per grid a constant. Only those grids entirely within the continental boundaries of the study area were selected. All grids lying partially in neighboring countries or over oceanic water bodies were eliminated, with the exception of two grids having more than 80% of their area within the continental boundaries of southern Africa.

2. Climatic data for each grid should be reasonably representative. If, for example, the climate station is at a low elevation and most of the grid is at a much higher elevation (thus the

TABLE 2. Descriptive statistics and correlations matrix.

	Correlation Matrix									
	Energy				Moisture					
	PEMIN	DIFPE	PEAN	PEMAX	PMAX	DIFP	ACTP	PAVM	PAN	AE
Species	0.8266	−0.5847	+	−0.3374*	0.8117	0.8057	0.7963	0.7270	0.7270	0.6715
Energy										
PEMIN		−0.4178	0.4833	−−	0.6192	0.6030	0.6335	0.5349	0.5314	0.5233
DIFPE			0.5252	0.9404	−0.6814	−0.6433	−0.6786	−0.7674	−0.7664	−0.7327
PEAN				0.7579	++	++	++	−	−	−
PEMAX					−0.5202	−0.4839	−0.5094	−0.6468	−0.6471	−0.6107
Moisture										
PMAX						0.9946	0.9619	0.9244	0.9228	0.8646
DIFP							0.9634	0.8873	0.8853	0.8309
ACTP								0.8687	0.8662	0.8294
PAVM									0.9996	0.9437
PAN										0.9439
AE										
PMI										
PWARM										
PMIN										
Drought										
Elevation										

* The probability that these correlations are not significant is at least less than 0.10, but not less than 0.0001.

Note: Unless otherwise noted (*), the probablity that these correlations are not significant is less than 0.0001. Further, only those coefficients with significance greater than 0.10 are noted. For those with significance less than 0.10, positive and negative signs are used to indicate the variable's directional influence. A double negative/postive symbol indicates the significance is less than 0.50.

TABLE 2. Continued.

	Correlation Matrix					Descriptive Statistics			
	Moisture								
	PMI	PWARM	PMIN	Drought	Elev.	Mean	Range	s.d.	R^2
Species	0.5801	0.5676	++	++	−	64.03	8–161	47.49	
Energy									
PEMIN	0.3270*	0.2799*	+	−	−0.4259*	25.78	14–48	8.36	0.683
DIFPE	−0.8070	−0.6544	−0.3650*	−0.4871	−0.3840*	101.02	62–177	24.98	0.342
PEAN	−0.4420*	−0.2747*	−0.3349*	−0.5994	−0.5940	902.82	589–1,379	147.74	0.043
PEMAX	−0.7670	−0.6191	−0.3537*	−0.5636	−0.5788	126.70	94–198	22.31	0.114
Moisture									
PMAX	0.8350	0.8072	++	+	+	114.37	15–246	54.62	0.659
DIFP	0.7928	0.7764	−	+	+	107.62	14–238	54.44	0.649
ACTP	0.7753	0.6996	−	++	+	61.38	15–131	28.89	0.634
PAVM	0.9598	0.8891	0.3640*	0.4791	+	48.55	5–102	22.58	0.529
PAN	0.9606	0.8889	0.3666*	0.4834	+	580.65	55–1,226	271.07	0.521
AE	0.8837	0.7873	0.3324*	0.4994	+	533.36	55–915	210.48	0.451
PMI		0.8959	0.4150*	0.5737	0.3294*	−33.38	−96–48	34.05	0.337
PWARM			0.3068*	0.4786	0.2574*	88.68	2–229	55.56	0.322
PMIN				0.7227	−0.2263*	6.95	1–27	6.08	0.003
Drought					+	9.11	1–12	2.15	0.001
Elevation						1,107.08	19–1,972	363.28	0.032

TABLE 3. Species diversity as a function of the minimum monthly potential evapotranspiration—a one-variable model (N = 60).

Analysis of Variance

Source of Variation	Degrees of Freedom	Sum of Squares	Estimated Variance	*F*-test		R^2	Standard Deviation
				F Value	*Pr* > *F*		
Model	1	90,944.197	90,944.197	125.16	0.0001	0.683	26.96
Error	58	42,143.74	726.62				
Corrected total	59	133,087.93					

Linear Regression

Parameters	Estimate	*T*-test Hypo *P* = 0	*PR* > *T*	Standard Error of Estimate
Intercept (*a*)	−57.013	−5.02	0.0001	11.36561976
PEMIN (*b*)	4.695	11.19	0.0001	0.41964134

Model: $Y = a + bX + e$, therefore: Species diversity = $-57.013 + 4.695X_{\text{pemin}} + e$ (s.e.).

majority of species are not necessarily found in low-lying areas), its use in the model was deemed inappropriate.

3. Because Palgrave (1977) was not able to consult the herbarium in Maputo, Mozambique, the distribution of species within Mozambique may be underrepresented. Therefore, grids within Mozambique were not included in the statistical analyses (except for areas contiguous to the Zimbabwe or South Africa borders).

RESULTS

Of the 1,365 species admitted by Palgrave (1977), 264 are edible. The map of species richness per grid (Map 3) when transformed into isoclines of increasing species richness (Map 4) displays a distinct west to east trend of increasing richness. A similar pattern can be seen in isometric maps of various climatic factors (see Fuller, 1980; Schulz & McGee, 1977; Tyson, 1977), most notably that of cloud cover. As can be seen, more edible plant species exist in the environs of the eastern escarpment region than along the southeastern/eastern coastal margin. This appears to accord well with what one might expect given the greater variety of vegetation associations in this region (Acocks, 1953; White, 1981, 1983).

STATISTICAL ANALYSES

Of the 166 equal-area grids, only 60 grids met all the criteria for inclusion in the statistical analyses. Descriptive statistics were run on this subset to determine whether it met the underlying assumptions and rigor necessary for use in an analysis of variance and linear regression. All variables were found to be "well behaved" and sufficiently normal in distribution.

Correlation matrix. Geographic variations in species richness are strongly correlated to both energy and moisture availability (Table 2). At a glance, the most significant variable is the minimum monthly potential evapotranspiration (PEMIN; $r = 0.8266$, $P < 0.0001$), followed closely by a suite of moisture variables. The variables DROUGHT and ELEVATION do not appear to directly influence species richness but are considered here because of their apparent influence on the energy and/or moisture variables.

Examining the energy variables more closely, it is noteworthy that annual potential evapotranspiration is not correlated to species richness. This is consistent with suggestions by earlier workers (e.g., Schulz & McGee, 1977) that annual values of potential evapotranspiration (or temperature) were not very meaningful when studying the influence of climate on the vegetation of southern Africa. Furthermore, the suite of energy variables are related to each other in such a fashion that as minimum monthly potential evapotranspiration (PEMIN) increases, there is a tendency for annual potential evapotranspiration (PEAN) to increase and monthly variability (DIFPE) to decrease. When monthly variability decreases, the maximum monthly potential evapotranspiration (PEMAX) also tends to decrease. Such a trend is also related to increases in the suite of moisture variables. This suggests that species richness tends to increase

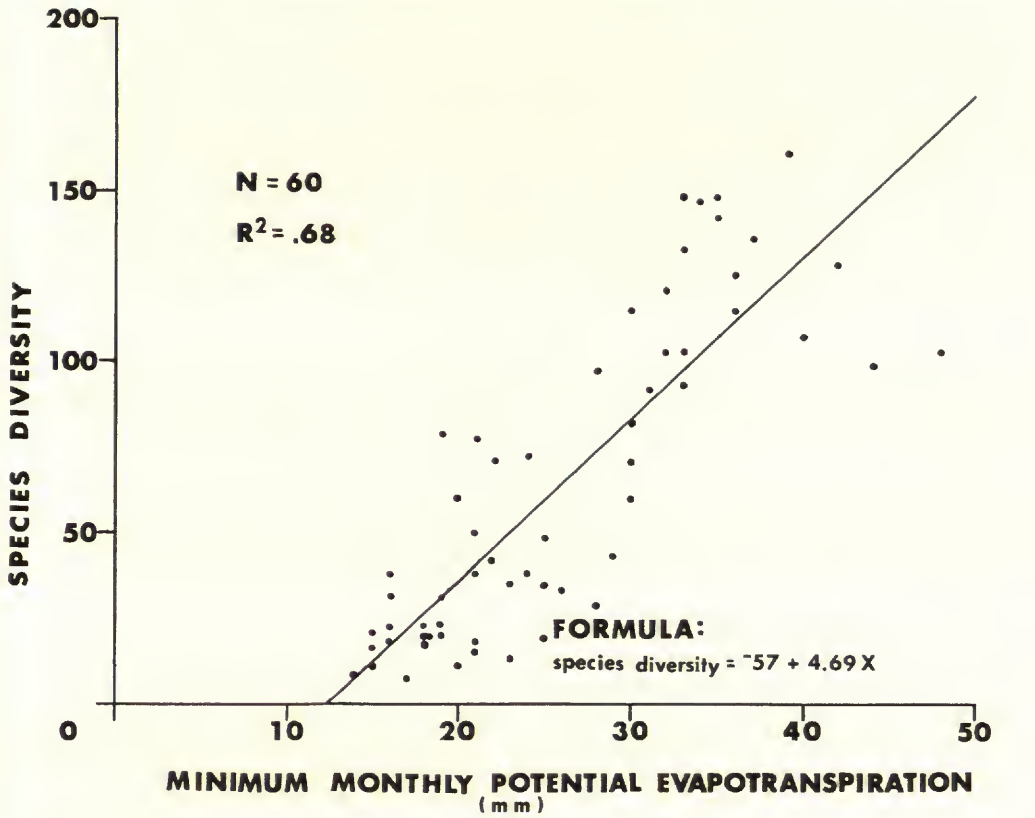


FIGURE 1. Graph of relationship between species diversity and PEMIN.

as the available energy (and moisture) for photosynthesis and plant growth increases and becomes more evenly distributed throughout the year. The energy variable most likely to discriminate this trend is the minimum monthly potential evapotranspiration (PEMIN).

In addition to being strongly correlated to geographic variations in species richness, all moisture variables (excluding PMIN) also manifest multicolinearity such that as one moisture parameter increases all others tend to increase. This relationship is most pronounced among the suite of moisture variables most highly correlated to species richness. These are:

a. maximum monthly precipitation (PMAX; $r = 0.8117$, $P < 0.0001$),
b. The range in monthly precipitation (DIFP; $r = 0.8057$, $P < 0.0001$),
c. actual monthly precipitation during the rainy season (ACTP; $r = 0.7963$, $P < 0.0001$), and less strongly by
d. average monthly precipitation and annual precipitation (PAVM and PAN, respectively; both with $r = 0.7270$, $P < 0.0001$).

Two of these variables are synonyms: DIFP, which is equal to the maximum monthly precipitation when some months of the year may have little if any rainfall ($r = 0.9946$, $P < 0.0001$); and PAVM, which is equal to annual precipitation ($r = 0.9996$, $P < 0.0001$). They will not be considered further. Among the remaining three, we find the following relationships:

a. PMAX is almost synonymous with ACTP ($r = 0.9619$, $P < 0.0001$).
b. PMAX is very strongly related to PAN ($r = 0.9228$, $P < 0.0001$).
c. ACTP is strongly related to PAN ($r = 0.8662$, $P < 0.0001$).

Clearly, as the maximum monthly precipitation (PMAX) increases, there is an increase in the intensity and duration of precipitation during the rainy (growing) season (ACTP), as well as in annual precipitation (PAN). This trend is highly

TABLE 4. Species diversity as a function of the maximum monthly precipitation (PMAX)—a one-variable model (N = 60).

Analysis of Variance

Source of Variation	Degrees of Freedom	Sum of Squares	Estimated Variance	F-test		R^2	Standard Deviation
				F Value	*Pr* > *F*		
Model	1	87,686.0312	87,686.0312	112.02	0.0001	0.659	27.98
Error	58	45,401.9021	782.791				
Corrected total	59	133,087.9333					

Linear Regression

Parameters	Estimates	*T*-test Hypo *P* = 0	*PR* > *T*	Standard Error of Estimate
Intercept (*a*)	−16.683	−1.98	0.0528	8.4385
PMAX (*b*)	0.7058	10.58	0.0001	0.0668

Model: $Y = a + bX + e$, therefore: Species diversity = $-16.683 + 0.706X_{pmax} + e$ (s.e.).

correlated to increases in species richness and is best reflected in the variable maximum monthly precipitation. Moreover, such increases are also related to an increase in the equitability and evenness of monthly energy parameters, suggesting that the maximum monthly precipitation may be a surrogate, but less precise, variable for minimum monthly potential evapotranspiration in explaining the geographic variations in species richness of edible woody plants.

The anomalous behavior of minimum monthly precipitation (PMIN) begs for interpretation. It is the only moisture variable showing no relationship to species richness. It is, however, strongly (and positively) correlated ($r = 0.7227$; $P < 0.0001$) with the variable DROUGHT, which also shows no relationship to species richness. Furthermore, neither of these variables is significantly correlated to any of the climatic variables most strongly correlated with species richness. In effect, lack of water during some months of the year (which in southern Africa is usually during winter) apparently has no influence on species richness; but, considering the importance of the minimum monthly potential evapotranspiration (PEMIN), low temperatures do. Going one step further, this suggests that the woody edible plants of southern Africa are comparatively well adapted to periods of drought (and/or are predominantly deciduous in character) but poorly adapted to low temperatures and/or frost. This is consistent with what is generally known about the vegetation of southern Africa.

The remaining moisture variables considered in this study do not appear to significantly affect species richness. The fact that they are slightly related to both minimum monthly precipitation and DROUGHT suggests, however, that these variables are also more a reflection of the physiologic character of the vegetation in southern Africa than of its species richness.

A final look at Table 2 finds that ELEVATION also shows no relationship to species richness nor, for that matter, does it appear to influence the suite of significant moisture variables. It is, however, moderately to weakly (and negatively) correlated to the suite of energy variables such that as elevation increases potential evapotranspiration parameters decrease. This is consistent with the concept of a standard lapse rate of declining temperatures with increasing elevation (Griffiths, 1976). (It is this phenomenon and not elevation per se that is associated with orographic precipitation.)

In summary, examination of the correlation matrix suggests that geographic variations in the species richness of edible woody plants in southern Africa correspond to geographic variations in the intensity, duration, and year-round equitability of the energy and moisture available for plant photosynthesis and growth. The independent climatic variables most likely to reflect this trend are the minimum monthly potential evapotranspiration and the maximum monthly precipitation. This may be due in part to the fact that the edible woody plants of southern Africa appear to be well adapted to periods of drought but poorly adapted to low temperatures.

Climatic models for predicting/explaining geographic variations in the species richness of edible

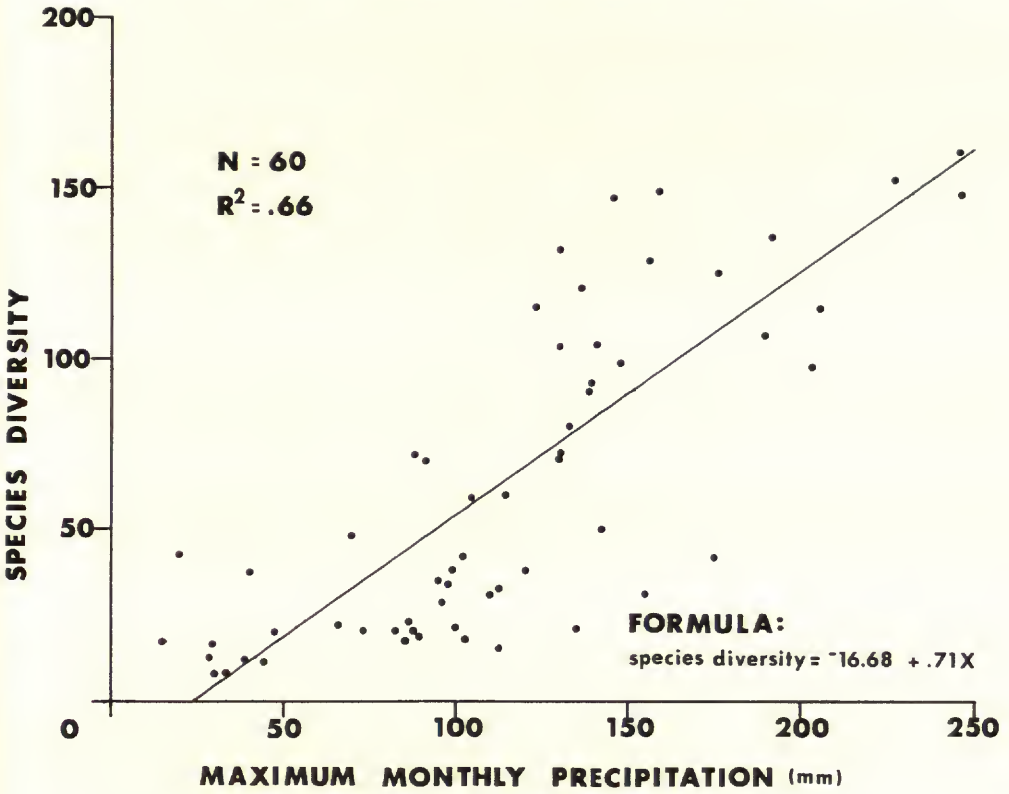


FIGURE 2. Graph of relationship between species diversity and PMAX.

woody plants. Analyses of variance and linear regressions were performed using various combinations of the energy and moisture variables discussed earlier. Not surprisingly, the best results were obtained using minimum monthly potential evapotranspiration (PEMIN) and/or maximum monthly precipitation (PMAX) as the independent climatic variables.

Minimum monthly potential evapotranspiration is the best single-variable model for predicting species richness. It has the highest explanatory power (R^2 = 0.683, i.e., 68%), the greatest precision (mean square error = 726.62), and the probability that this relationship occurred by chance is less than 0.0001 (Table 3). In Figure 1, the closeness of fit of the model is displayed as well as the equation generated by linear regression. It is of interest here that the x-intercept value (which is more ecologically relevant than the negative y-intercept) suggests that the environment in southern Africa is not conducive to the support of woody edible plants in regions where the minimum monthly potential evapotranspiration falls below 12.5 mm.

Maximum monthly precipitation is the second best single-variable model. It is slightly less precise than minimum monthly potential evapotranspiration (mean square error = 782.79) and explains only 66% of the geographic variation (R^2 = 0.659). Again, the probability that this relationship occurred by chance is less than 0.0001 (Table 4). The closeness of fit and the equation generated by the linear regression are displayed in Figure 2. Furthermore, the x-intercept in this model suggests that environments in southern Africa where maximum monthly precipitation is less than approximately 25 mm are not conducive to sustaining woody edible plants. It is of interest here that Schulz & McGee (1977) suggested 25 mm of monthly precipitation to be the cutoff point for inclusion in the rainy/growing season.

Clearly, the minimum monthly potential evapotranspiration and the maximum monthly

TABLE 5. Species diversity as a function of the minimum monthly potential evapotranspiration (PEMIN) and the maximum monthly precipitation (PMAX)—a two-variable model (N = 60).

Analysis of Variance

Source of Variation	Degrees of Freedom	Sum of Squares	Estimated Variance	*F*-test		R^2	Standard Deviation
				F Value	*Pr* > *F*		
Model	2	110,350.636	55,175.318	138.32	0.0001	0.829	19.97
Error	57	22,737.297	398.899				
Corrected total	59	133,087.933					

Linear Regression

Parameters	Estimates	*T*-test Hypo *P* = 0	*PR* > *T*	Standard Error of Estimate
Intercept (*a*)	−61.2794	−7.26	0.0001	8.4434
PEMIN (b_1)	2.9846	7.54	0.0001	0.3959
PMAX (b_2)	0.4228	6.97	0.0001	0.0606

Model: $Y = a + b_1X + b_2X + e$, therefore: Species diversity = $-61.2794 + 2.9846X_{\text{pemin}} + 0.4228X_{\text{pmax}} + e$ (s.e.).

precipitation individually explain a significant portion of the observed geographic variation in species richness, but together, as a two-variable model, they explain more. As can be seen in Table 5, the explanatory power rises to 83%, precision increases (from >700 to <400), and the probability that this relationship occurred by chance is still less than 0.0001. This is further emphasized when we compare the closeness of fit between actual species richness per grid and the species richness per grid predicted from the linear regression equation (Fig. 3). In effect, whenever the minimum monthly potential evapotranspiration and/or the maximum monthly precipitation increase, there is a strong tendency for species richness to increase. This tendency, however, is neither absolute nor necessarily of uniform magnitude:

$$\text{species richness} = -61.28 + 2.98X_{\text{pemin}} + 0.42X_{\text{pmax}} \pm e \text{ (s.d.)}$$

Models using three or more climatic variables were also generated. However, the small increase in explanatory power (8 variables almost achieved an R^2 of 0.85), coupled with a reduction in precision, indicates that the two-variable model is statistically superior to more complex climatic models in addition to being more elegant and parsimonious.

In summary, 83% of the observed geographic variation in species richness is predictable given knowledge of only two climatic parameters: the minimum monthly potential evapotranspiration and the maximum monthly precipitation. When combined in a two-variable statistical model, they appear to be measuring the photosynthetic potential of the environment that is determined by climate: the intensity and duration of both usable incoming solar energy and effective precipitation (precipitation minus water demand) during the growing season. Improvement of this model should concentrate on embracing gradients of other abiotic and biotic factors that influence plant photosynthesis, growth, or reproduction.

CONCLUSION

The diversity of humanly edible woody plant species changes across the landscape of southern Africa, manifesting a west to east trend of increasing species richness (Maps 3, 4) that is similar to trends observed in some climatic variables, most notably in the number of days with cloud cover. It is lowest in the Namib/Namaqualand/Cape/Kalahari regions and highest in the eastern escarpment and the southeastern and eastern coastal regions. This trend confirms field impressions and is consistent with what might be expected given the pattern of vegetation types and associations across this area (Acocks, 1953; White, 1981, 1983; Brennan, 1978; Goldblatt, 1978; Werger, 1977). This also suggests that it might be possible to characterize particular vegetation types and associations in terms of their human plant food dietary resources after appro-

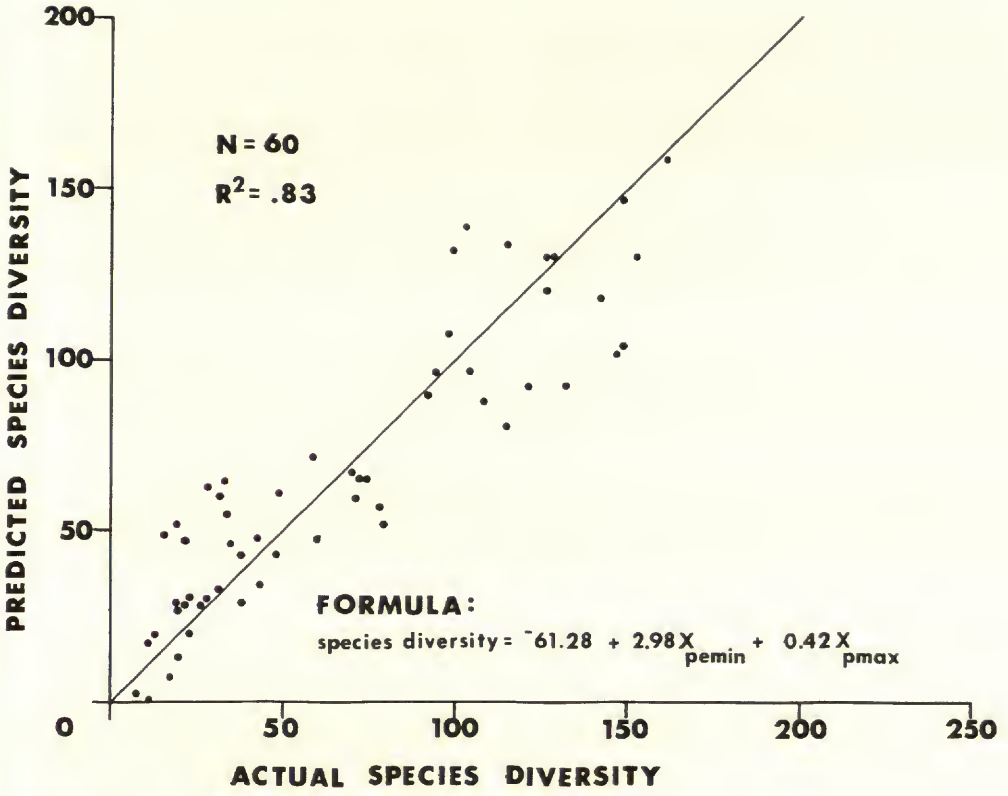


FIGURE 3. Graph comparing predicted vs. actual species diversity.

priate consideration, on a meso- or microscale of analysis, of such factors as plant type, seasonality, and abundance (Peters et al., 1984).

Statistically and theoretically, this first order, macroscale study suggests that geographic variations in the intensity and duration of energy and moisture for plant photosynthesis during the growing season accounts for most (83%; $P < 0.0001$) of the observed spatial variation in plant species richness across southern Africa:

$$\text{Plant Species Richness} = \int\left[\Delta \text{ ENERGY} + \Delta \text{ MOISTURE} \pm (\text{other abiotic or biotic factors})\right]$$

The actual climatic variables most closely related to changes in species richness in southern Africa were the minimum monthly potential evapotranspiration and the maximum monthly precipitation. As these factors, individually or together, increase in value, species richness increases and vice versa. Interestingly, the absence of water during some months of the year is not statistically related to species richness, evidenced by the lack of any correlation between species richness and the minimum monthly precipitation. This is, however, consistent with what might be expected from a flora that is physiologically well adapted to periods of drought but poorly adapted to low temperatures or frost. Seen in this light, geographic variations in species richness may exist simply because fewer and fewer plant species have the physiological capabilities to photosynthesize, let alone grow and reproduce, as the "photosynthetic potential" decreases across southern Africa. This is consistent with the idea that climate regulates plant growth and the distribution of both plant types (Box, 1978; others) and vegetation associations (Walter, 1979; others).

Keeping in mind the limitations of this study and that absolute values are likely to be valid only within southern Africa, the statistical model should prove useful in generating discrete rela-

tive gradients of increasing potential species richness of edible plants for elsewhere in Africa. This model should prove to be most useful in areas sharing similar floristic and climatic characteristics with southern Africa, i.e., the summer rainfall, semiarid regions of Africa.

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NOTES ON THE DISTRIBUTION AND RELATIVE ABUNDANCE OF *SCLEROCARYA BIRREA* (A. RICH.) HOCHST. (ANACARDIACEAE)[1]

CHARLES R. PETERS[2]

ABSTRACT

Sclerocarya birrea is widespread at low to medium elevations in the Sudano-Zambezian and immediately adjacent phytogeographical regions of Africa. The species is also reported to be common at scattered localities from the Sudan through coastal Natal and northern Namibia. The tree is at least somewhat drought resistant and apparently a reliable annual fruiter. The fruits and oil seeds traditionally provided staple foods in parts of southern Africa, and the seeds may still provide critical nutrients during drought and famine.

RÉSUMÉ

Sclerocarya birrea est répandue à des altitudes basses ou moyennes dans la région Soudano-zambézienne et dans les régions phytogéographiques directement voisines en Afrique. On signale également que cette espèce est commune dans des localités dispersées du Soudan au nord de la Namibie en passant par le littoral du Natal. Cet arbre est au moins assez résistant à la sécheresse et donne en apparence régulièrement des fruits chaque année. Les fruits et les graines oléogineuses étaient des sources traditionnelles pour la nouriture de base dans le sud de l'Afrique, et elles peuvent fournire des substances nutritives essentielles pendant les périodes de sécheresse ou de famine.

Species with edible fruit that also possess nutritious oil seeds are of special interest to ethnobotanists and wildlife ecologists. One such species is the usually dioecious deciduous tree *Sclerocarya birrea* (A. Rich.) Hochst.

Sclerocarya birrea belongs to the mango family (Anacardiaceae) and the fruit is a plum-sized drupe with a leathery rind like a mango and a juicy fibrous pulp which is difficult to separate from the stone or nut (Eggeling & Dale, 1952; Palmer & Pitman, 1972). The tart thirst-quenching pulp is exceptionally high in vitamin C (Carr, 1957; Wehmeyer, 1966). It is consumed raw, boiled down to make a syrup for sweetening porridge, and brewed to make an intoxicating drink (Dalziel, 1937; Eggeling & Dale, 1952; Irvine, 1961; Palmer & Pitman, 1972). The walnutlike stone has 2–3 (1–4) plugged cells, each containing a seed, which are difficult to extract intact but are high in fat (56–61%), protein (28–31%), phosphorus (Ferrão, 1960; Busson, 1965; Wehmeyer, 1966), magnesium, copper, zinc, thiamin, and nicotinic acid (Wehmeyer in Shone, 1979; Arnold et al., 1985). Ferrão (1960) also reports that lysine is the limiting amino acid. The soft oily seeds are eaten raw, pounded or ground into powder for soup (plus other foods), and stamped to form a cake which can be eaten alone (Palmer & Pitman, 1972; Williamson, 1975; Krige, 1937). Krige (1937) reports that *S. birrea* was once an important staple food in drier regions of the northern Transvaal and that in the lowveld of the eastern Transvaal (near Kruger National Park) the Phalaborwa subsisted largely on the stored nuts during the winter dry season. Cunningham's (1985) research shows that on the Maputoland coastal plain in Natal the nuts are still stored and provide a major source of protein during drought periods. They have also been used as a famine food in Zambia and Tanzania [*Bullock 1316, 3435* (K)]. Palmer & Pitman (1972: 226) report that (as told to Dr. van der Merwe of the Nutrition Research Institute, Pretoria) the oil from the seeds has preservative properties. The Venda in the northeastern Transvaal use it in preparing meat for storage. Dried and stored in a cool place, such meat is said to keep up to one year. The Venda also pound the seeds with lean sinewless meat and the mixture is shaped into cakes that are dried and stored. This is analogous to pemmican,

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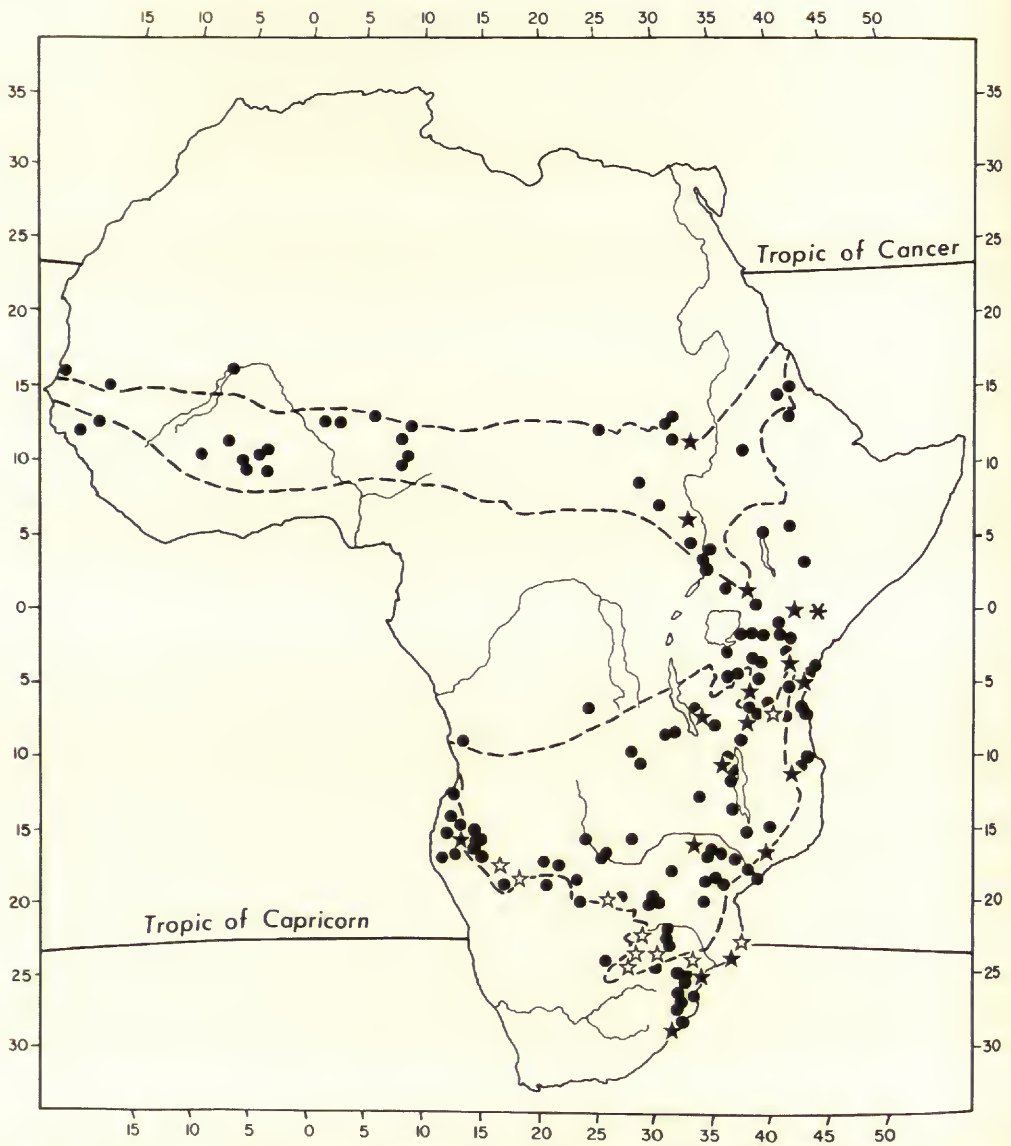

FIGURE 1. Geographic distributions of *Sclerocarya birrea* (A. Rich.) Hochst. (black stars & dots, cf. Appendix I) and *Sclerocarya gillettii* Kokwaro (asterisk near the equator in east Africa). Stars denote presence of localities where the trees are relatively common or scattered but frequent: black stars based on herbarium vouchers; open stars based on other reports, see text. The Zambezian and Sudanian Phytochorial Regions (cf. White, 1981) are indicated by dashed lines. The map is an equal area projection.

although it is called *Venda biltong*. (See Shone, 1979, for additional notes on the seed's nondrying type oil.) All of this testifies to the actual or potential importance of *S. birrea* for the indigenous diet. It perhaps comes as no surprise then that in some parts of southern Africa this tree was once said to have been venerated (Fanshawe, 1962; Palmer & Pitman, 1972).

One season's productivity for four trees on a citrus estate, measured by Quin (1959) near Zebediela in the northern Transvaal, ranged from 21,667 to 91,272 fruits. The year sampled by

Quin was a relatively dry one (Peters & Maguire, 1981). Moss & Taylor (1983) report that one season's productivity for 11 trees at Gabane Village in Botswana ranged from 17,445 to 66,822 fruit. Shone (1979) reports a yield of 9,601 fruit for a tree in the northeastern Transvaal. The annual productivity of smaller trees in apparently less favorable circumstances may be as high as 2,000 fruit (pers. obs., 1984, with L. Wadley on a single tree in the western Transvaal). Thus it would appear that wherever this tree is relatively abundant, the fruit constitutes an important seasonal resource for vitamin C, food energy, fat, protein, and minerals.

At present we have very little ethnobotanical, ethological, or productivity information on *Sclerocarya birrea.* Its significance as an indigenous food resource should be more widely recognized, however, and a more general account of the plant's geographic distribution and habitats could help in evaluating its potential dietary importance elsewhere in Africa.

Methods

My primary sources for ecological information were the regional floras, a few forestry manuals, and ethnobotanical/ethological studies, but especially the notes accompanying specimens deposited by plant collectors in the Kew and British Museum herbaria. The carpological collections were only partly analyzed and have not been included in construction of the preliminary distribution map (Fig. 1). The vouchers for the map are cited by country, first-order administrative unit where necessary, and the collector in Appendix I. Mapable coordinates were obtained from the *U.S. Board on Geographic Names* gazetteers, *The Times Atlas of the World Series,* the *Michelin* 1 : 4,000,000 Maps of Africa, and Dianna Polhill's unpublished *Index of Collecting Localities for the Flora of Tropical East Africa.* Gillett (1972) was an aid for Schimper's 1842 Abyssinicum (Ethiopian) specimens, and Wickens (1972) for Schweinfurth's 1869 Sudanese specimens. The CCTA/CSA *Climatological Atlas of Africa* (Jackson, 1961) and *Goode's Atlas* (Espenshade & Morrison, 1983) were used to estimate the approximate range of average annual rainfall experienced by *Sclerocarya birrea* on a gross geographic scale. Werger's frost map of southern Africa (Werger & Coetzee, 1978) served a similar purpose.

This particular study was undertaken as part of a larger ongoing survey of the several hundred edible wild plants that are found in eastern and southern Africa (Peters & O'Brien, 1981; Peters et al., 1984).

Results

Following Kokwaro & Gillett (1980) and Kokwaro (in press), two species of *Sclerocarya* are recognized here: *S. birrea* (A. Rich.) Hochst. and *S. gillettii* Kokwaro.

Sclerocarya birrea is widespread in deciduous woodland and wooded grassland, from Senegal to Ethiopia in the north, from Ethiopia southward to Natal in the east, and from Natal through northern Namibia into Angola in the south. The geographical distribution of *S. birrea* is depicted in Figure 1 (based on the vouchers listed in Appendix I). In East Africa, *S. birrea* ranges in elevation from 5–1,800 m, the lower elevations near the coast being apparently occupied only by subsp. *caffra* (Kokwaro & Gillett, 1980; Kokwaro, in press). Considering its entire continental geographic distribution, *S. birrea* experiences a range of average annual rainfall of ca. 200–1,500 mm.

Kokwaro & Gillett recognize three subspecies of *Sclerocarya birrea*: west African subsp. *birrea,* distributed from Senegal to Ethiopia, in the east on down into Tanzania; east African subsp. *multifoliolata* (Engl.) Kokwaro, known only from central Tanzania (ca. Ngorongoro/Serengeti to Ruaha National Park); and south African subsp. *caffra* (Sond.) Kokwaro, found from Namibia, Angola, and southern Zaire to Natal and Tanzania, up as far as southeast Kenya. All three subspecies overlap in central Tanzania, southeast of Lake Victoria. The fruits of the three subspecies appear to be indistinguishable. I have not checked all of the subspecies determinations carefully enough to plot their distributions separately in Figure 1, but I should also point out that the geographic distributions of the subsp. *birrea* and *caffra* probably correspond remarkably closely with the Sudanian and Zambezian phytochoria, respectively (also see Hutchinson et al., 1958; Fernandes & Fernandes, 1966).

Sclerocarya gillettii is a rare dwarf species, at present known only from the bushlands of central east Kenya, approaching Somalia (ca. 200–400 mm average annual rainfall). The area is marked with an asterisk in Figure 1. There are apparently no specimens collected as yet from

Somalia. It is perhaps not unexpected that eastern Africa is the region with both species and subspecies diversity. Perhaps it might repay someone to carefully compare specimens from the Kalahari and Kenya/Somalia for a possible arid zone disjunction.

As can be seen in Figure 1, as a broad generalization *Sclerocarya birrea* is largely confined to the Sudanian and Zambezian zonobiomes or phytogeographical regions. Following White's (1976) chorological designations, *S. birrea* is also present in the easternmost Lake Victoria Basin regional mosaic, the southern half of the Somalia–Masai regional phytochorian, and the east coast (Zanzibar–Inhambane plus Tongaland–Pondoland) regional mosaics. There are also outliers in the dry northwesternmost Kalahari Highveld transition zone and the adjacent Karoo–Namib phytochorian.

Most of the information on the relative abundance or density of *Sclerocarya birrea* had to be obtained from the herbarium vouchers listed in Appendix I. Information on this is generally lacking for western Africa, but for eastern and southern Africa the following information was obtained. In Sudan, Simpson [*7738* (K)] reports that it is frequent near the Nuba Mountains, and Francis [*82* (K), not cited in Appendix I] reports that near Galabat Reserve (exact locality still uncertain) it is often locally dominant near lower hill slopes at ca. 914 m. Andrews [*A2038* (K)] notes that it is common on the Juba–Torit road, but the habitat is not specified. In Kenya it is reported to be a common tree in well-watered places within Meru National Park, e.g., apparently Fig Tree Drift river crossing, ca. 580 m elevation [*Ament 567* (K)]. In central Uganda it is reported to be a common large tree in dry forest at 122 m [*Thomas Th. 2198* (K)]. Brenan (1949) states that it is frequent to common from the coast of Tanzania to Lake Tanganyika. Greenway [*4218* (K)] notes that near the coast (15 m elevation) in Tanga District, it is common but scattered on a dark brown soil overlying a red earth, and that near Kilimanjaro in Chala Crater [*4456* (K)] at 1,097 m elevation it is common but scattered on a dark brown volcanic soil. Burtt [*1858* (K), exact locality still uncertain] reports that it is common in Central Province. In western Tanzania, Michelmore [*737* (K)] reports that it is a common tree in the Rukwa Rift Valley. Moving to the east again, in Ruaha National Park, Greenway & Kanuri [*14679* (K)] report that it is locally common on rocky ridges in open to closed woodland. In Mikumi National Park it is also common in some places (G. Norton, pers. comm.). In southeastern Tanzania, just west of the Mbangala River, Milne-Redhead & Taylor [*7684* (K)] note that it is the dominant tree in woodland at 390 m elevation. In Malawi, Chapman [*79* (K)] reports that in the Rumpi Boma area, the mopane forest growing on grayish sand is 60% *Colophospermum mopane* and 40% *S. birrea*, and further that *S. birrea* is also common in the Rumpi–Njakwa region. Williamson (1975) states that it is common near Nsanje. In northeast Zimbabwe, near the Mkumburu River, Phipps [*2397* (K)] reports that it is common on alluvial soil at 512 m elevation. In southern Angola, Gossweiler (1950) reports that it is frequent from the land of Quilengues to Dirico (not marked in Fig. 1), and Henriques [*213* (BM, K)] notes that it is abundant near Humbe. In northern Namibia, Dinter (1909) states that it occurs everywhere in north and northwest Grootfontein, and that where limey, chunky (?calcareous, less sandy), mixed black soil dominates, it is a very frequent tree and, further, that Schinz found it very frequent in Ovamboland.

It is a common tree in several areas of the Transvaal of South Africa. Acocks (1975) recognizes it as the defining tree in two of his mixed bushveld subtypes in the western and northern Transvaal (part of White's, 1983, south Zambezian undifferentiated woodland). Four areas are noted by Acocks: 1) on the deep red sands of the lower slopes of the Waterberg Mountains between the Mogol and Matlabas rivers; 2) on the rolling granite countryside of the Crocodile-Elands Valley north of Rustenburg; 3) on wide granite ridges between thorn-filled valleys on the gentle northern slopes of the Pietersburg Plateau; and 4) near Zebediela. For the last area Peters & Maguire (1981) report that it can be fairly frequent in the mixed bushveld around Potgietersrust. My personal observations in this case are that it is locally common but scattered on the gentle lower slopes and adjacent plains associated with the Hanglip-Strydpoort Mountains and Nyl River Valley (also see Peters & Maguire, 1981, fig. 1). Palmer & Pitman (1972: 226) note that it is one of the most common trees in the eastern Transvaal lowveld. With regard to this area, van Wyk (1972, 1974) reports that: 1) it is plentiful in the undulating granite bushveld and fairly open smaller-tree savanna of the western portions of Kruger National Park; and 2) that it is abundant (van Wyk, 1984) on the basalt plains

west of the Lebombo Range between the Olifants and Crocodile rivers [see van Wyk's (1984) vegetation map of Kruger National Park]. Werger & Coetzee's (1978, fig. 49) account indicates that the plains are characterized by clayey basaltic soil, and they include a photo (fig. 50) of a tall tree savanna of predominantly scattered *Sclerocarya birrea* and *Acacia nigrescens* on the eastern foothills of the Lebombo Mountains (more or less level areas?) with apparently similar clayey basaltic soil. Along the coastal lowlands in Natal, Ward [*1534, 5256* (K)] reports that *S. birrea* is common to frequent on sandy soil (specimen *1534* is not cited in Appendix I, because the exact locality is uncertain). *Sclerocarya birrea* is also reported to be common in some areas on the sandy coastal plain of Mozambique [*Faulkner 2* (BM, K), *Gomes e Sousa 2051* (K), *Swynnerton 6514* (BM)]. Gomes e Sousa [1949 (1951), 1967] reports that it is very common south of the Save River in Mozambique, particularly on the coastal plain, on both sandy and clayish or loamy soils in open woodlands, and that in the areas around Maputo (Lourenço Marques), Morrumbene, and Inhambane, plus more generally over the coastal plain of the districts of Inhambane and Gaza, it is very abundant, becoming the dominant tree over large areas. He also notes that the propagation of this species is "favored" by the indigenous people for its fruit. I can add that I saw the fruit of *S. birrea* also play an important role in the diet of the people of Inhaca Island, near Maputo, on a brief visit there during the fruiting season of 1986.

Some judgments can be made about the general habitat and climatic preferences of this species. In Botswana, Moss & Taylor (1983) note that *Sclerocarya birrea* shows a soil preference for well-drained sands and loams. This would appear to explain its more widespread relative abundance in association with hills, rocky ridges, alluvial soils near rivers, and coastal plains.

Except perhaps for its penetration into the Transvaal, the general south African distribution of this species suggests that frost is an important limiting factor. In point of fact, it does not go into the highveld, being generally limited to the warmer frost-free areas, as the young plants are tender to frost (Palmer & Pitman, 1972; von Teichman, 1982). Exceptional years can even see damage to adult trees in the lowveld, as van Wyk (1974) reports that in Kruger National Park during the winter of 1964 large trees were badly injured and even branches of 15–25 cm in diameter were killed off by temperatures of −4°C.

Judging by the geographic distribution of the site records indicating the tree is relatively common or frequently occurring, the preferred range of average annual rainfall is ca. 500–1,200 mm, with less certainty about the upper end of the gradient. One apparent exception to this is the open *Sclerocarya* veld occurring on the wide ridges of the northern slopes of the Pietersburg Plateau under a rainfall of 350–400 mm per annum, but here the trees are reported to be "small" (Acocks, 1975). Under favorable conditions the mature tree can reach 20 m (Lebacq & Dechamps, 1967; Shone, 1979), but over the broader portion of its geographic range the maximum height is probably closer to ca. 10 m (Palmer & Pitman, 1972: 1189; various vouchers).

In the only note on succession known to me, van Wyk (1972: 4) reports that the previously subdominant *Sclerocarya birrea* already has become, or is fast becoming, the dominant species over quite large areas on the basalt plains of southwestern Kruger National Park. *Acacia nigrescens* was the most important tree in the outstanding grasslands found on these southern plains. *Combretum imberbe* was second in prominence. Both of these species have been dying off for many years, and van Wyk further states that this is most possibly due primarily to a shortage of moisture caused by overgrazing and veld fires, but also to woodborers, particularly in the case of *A. nigrescens*. *Sclerocarya birrea* can also tolerate ringbarking by elephants to a much greater degree than can *A. nigrescens* (van Wyk, pers. comm. in Werger & Coetzee, 1978: 317).

Concluding Comments

Considering the apparent nutritional value of the fruit of this tree, it is perhaps surprising that we know virtually nothing about its absolute density (number of trees/hectare or total number of trees per high-frequency area) and productivity over time. Palmer & Pitman (1972: 226) point out that the "flesh and kernel together make this fruit one of the most life-giving borne by any tree, wild or cultivated." Certainly in semiwild or more natural (protected) areas, a great variety of mammals (including elephants and *Papio* baboons) still enjoy its benefits, but from the point of view of human nutrition today, it may not appear to be very important. This might be an erroneous and unfortunate conclusion, however. Near villages in areas where it appears to be un-

derexploited it can still be an important food item for children (Moss & Taylor, 1983; also see Williamson, 1975). In this regard its human value may still be very high, perhaps more so, given the nutritional problems of these modern times.

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APPENDIX I
LOCALITIES OF *SCLEROCARYA BIRREA* SPECIMENS

MAURITANIA. Near Selibaby, *Popov 74* (BM).

SENEGAL. St. Louis, *Perrotet 150* (BM). Walo [Qualo], *Heudelot s.n.* (K). Niokolo Koba National Park, Mt. Assirik, *Tutin 22* (K).

GUINEA-BISSAU. Gabu: Coiada, *Santo 2504* (K).

MALI. Timbuktu, *Chevalier 1207* (K).

UPPER VOLTA. Near rock of Sindou, 50 km W of Banfora, *Leeuwenberg 4331* (K). 17 km east southeast of Boromo, *Sihronen 130* (K).

GHANA. Upper: Near Bawku, *Morton A4223* (K); Nobiga, Moshi, *Irvine 4610* (K); Walemboi to Wahabu, *Kitson 649* (K). Northern: Bantala, Kulpawn River flat, *Kitson 839* (K); Yendi, *Dalziel s.n.* (K).

NIGER. Maradi Province: Zinder road, 29 miles from Maradi, *Hall 384* (K). Dosso: Dallol Tuli-Malaukarvi area, *Virgo 15* (K).

NIGERIA. Northwestern: Soko To, *Gilman 3* (K), *Ijomah FHI 26467* (K). Northeastern: Nguru, Karasuwa Village area, *Onochie FHI 23352* (K); Bauchi, *Lely P139* (K); Bauchi, Zalanga Mission Compound, *Wit, Gbile & Daramola FHI 51168* (K); Bauchi, Gombe, between mile posts 148 and 147 on Gombe-Yola road, *Latilo, Okeke & Odewo FHI 69387* (K).

SUDAN. Darfur: Jebel Marra, Gandatour-Kalokitting, *Wickens 1294* (K). Bahr El Ghazal: Aweil-Nyamlell road, ½–1 mile SW of Mapare Village, *Hoyle 604* (BM); Seriba Ghattas [Jur], *Schweinfurth 1327, 1488* (K); Yirol-Lau road, *Andrews A666* (K). Kordofan: Jebel Muquisim, near Mahbub, *Wickens 356* (K); Jebel Ghubsh, near Khuwei, *Wickens 374* (K); near Dilling, *H. M. & A. S. Broun 1291* (K); near Nuba Mts., *Simpson 7738* (K). Equatoria: Bahi el Jebel, near Kero [Hill], *Muriel S84* (K); Liria, *Andrews A2038* (K). Blue Nile: Abu Shendi, *Muriel L50* (K).

ETHIOPIA. Gemu-Gwefa [Gofa]: Lower Omo Valley, Chobwe (Mursi), *Turton 98* (K). Sidamo: Ridge near Tula (slopes NW of Tula), *Gillett 14868* (K); 201 km S Langano Hotel, road turn-off to Arba Minch, *Ash 1599* (K). Begemdir: Tacaze [Tekeze] River Valley, below Dscheladscheranne [Djeladjeranne], *Schimper 610 [1842]* (K). Eritrea: 4 miles N of Barentu, *Hemming 1020* (BM); Keren, *Steudner 616* (K).

KENYA. Eastern: Moyale, *Gillett 13726* (K); Fig Tree Drift, Meru National Park, *Ament 567* (K); 40 miles S of Kitui, *Bogdan AB4379* (K); Machakos, *Langdale-Brown 21* (K); Chyulu Hills, ca. 5 km N of Tsavo National Park W Ranger Post, *Gillett & Stearn 21635* (BM, K). Coast: N Mombasa, between Vipingo & Takaungu, *Bally B4707* (K); Mwachi, *Graham 1606* (K). Central: Tebere, Kirinyaga District Cotton Research Station, *Robertson 2045* (K). Rift Valley: Oloibortoto, about 25 miles W of Lake Magadi in the foothills of the Nguruman Escarpment, *Glover & Samuel 3251* (K); Kajiado District, Soda Co. Water headworks, *Gillett 16787* (K); Haralanna River, Nguruman Escarpment, *Bally B3180*; near Lenyora, Nguruman Hills, *Bally B3824, B3830* (K); Egerok [Keekorok], Mara Masai Reserve, *Bally B5443* (K); Baringo District, 17 km Marigat-Kabarnet, *Leippert 5257* (K); W Pokot District near Kongelai, *Tweedie 3408* (K).

UGANDA. Bugisu: 4 km E of Karita, *Leippert 5086* (K). Karamoja: near Emoruayaberry [Moruangaberu], *Dyson-Hudson 118* (K); Kakumongole, *Thomas Th.2198* (K). Lango: Serere, *Chandler 1106* (K). Madi: Metuli, *Eggeling 1233 [877]* (K); Aiyuge River, Gulu-Pakelli road, *Eggeling 1225 [862]* (K); Laropi Escarpment, *Tothill T.2497* (K).

ZAIRE. Kasai Oriental: Mwene Ditu, *Liben 3843* (K). Shaba: Kalebuka, 8 km NW of Kapolowe Mission, *Malaisse 6693* (K); Lufira [River], 60 miles N of Elisabethville, *F. A. Rogers 10309* (BM, K).

TANZANIA. Tabora Province: Mteshi, *Bullock 2306* (K); on a track W of Ziba-Simbo road, *Lawton 2138* (K). Mwanza Province: Nyambiti, *Tanner 1266* (K). Mara Province: Kiagata, *Tanner 4006* (K). Arusha Province: Kline's [Klein's] Camp, near Loliondo, *Brooks 83* (K); Endulen, Ngorongoro, *Herlocker 540* (K); Ndala River, Lake Manyara National Park, *Greenway & Kirrika 11155* (K); Bagoyo Ridge, Manyara, *Richards 24314* (K). Kilimanjaro Province: Lake Chala [crater], *Greenway 4456* (K); Moshi, Himo-Chala area, *Bally B548* (K). Tanga Province: Mtimbwani, *Greenway 4218* (K); Korogwe Teachers Training College, *Archbold 59, 68* (K); 25 miles SW of Mombo, *Leippert 6217* (K); Kideleko, *bin Mohamedi 8619* (K); Msubugwe Forest, *Tanner 18* (K); near Pangani, *William 531* (K). Coast: Bagamoyo, *Kirk s.n.* (K); *Harris BJH2472* (K). Morogoro Province: Uluguru Mts., *Bruce 122* (BM, K); Mikumi National Park, at Mkata River 5 km WNW of Park Headquarters, *Bjørnstad AB1212* (K). Singida Province: Ntwike, by the Wembere Steppe, *Michelmore 799* (K). Dodoma Province: Mnenia, *Phillips in B. D. Burt 1889* (K); Mpwapwa Hills, *B. D. Burtt 4808* (K), *Hornby 358* (K); Ilangali, *Magogo & Ruffo 688* (K). Iringa Province: 50 miles from Iringa on the Dodoma–Iringa road, *Verdcourt 3077* (K); E part of Ruaha National Park, ca. 5 km N of Msembe, *Thulin & Mhoro 625* (K); E part of Ruaha National Park, near Makindi, *Thulin & Mhoro 683* (K); Ruaha National Park, track to the Ruaha River ferry, *Richards & Arasululu 26374* (K); Ruaha National Park road junction and [sic] the Idodi road, *Greenway & Kanuri 14679* (K). Mbeya Province: Manda, *Bullock 3435* (K); Soa [Sao] Hill—Madibira road, *Richards 17340* (K); 74 miles E of Mbeya, Iringa road, *Boaler 295/3* (K); Rukwa Rift Valley, *Michelmore 737* (K). Mtwara Province: 40 km & 45 km W of Lindi, *Schlieben 5401, 6226* (BM); just W of the Bangala [Mbangala] River, *Milne-Redhead &*

Taylor 7684 (K); Lissekesse [Lisekese], *Gillman 1199* (K).

Malawi. Northern: Manganja [Manganga] Hills, *Meller s.n.* (K); ca. 10 miles from Katowo & past Khuramaji along the road which follows the S side of Vwaso Marsh, *Chapman 79* (K); 1 mile E of Rumphi, St. Patrick's Mission, *Pawek 13789* (K); W shore of Lake Nyassa, Mankambira, *Kirk s.n.* (K). Central: Chitala, *Greenway 6375* (K). Southern: Zomba, *Purves 230* (K).

Zambia. Northern: Kaputa, *Bullock 1316* (K); Chiengi, *Bullock 1240* (K); Luangwa Valley, Mfuwe, *Astle 4158* (K). Southern: Victoria Falls, *Wild 3200* (K); Mapanza Mission, *Robinson 948* (K). Western [= Barotseland]: Zambezi River, Sesheke, *Mutimushi 3676* (K); near Zambezi River, Sesheke Boma [Pan], *White 1994* (K); near Senanga, *Codd 7357* (K).

Angola. Cuanza Norte: Cambambe-Dondo, *Gossweiler 9348* (BM, K). Benguela Province: Catengue, *Gossweiler 12321* (BM). Moçâmedes Province: Cahinde [Cainde], *Gossweiler 10731* (BM). Huila Province: Chimbolelo [Tchimbolete], *Grandvaux Barbosa & Gouveia 10715* (BM, K); Humbia, base of Serra da Chela, *Exell & Mendonça 2056* (BM). Cunene Province: Lucambo Hill, Mupa, *de Menezes 1347* (K); near Evale, *de Menezes 1390* (BM, K); near Mulondo, *de Menezes 905* (K); Quiteve, by the trail from the river, *Grandvaux Barbosa 10818* (BM, K); between Humbe and Roçadas, *Raimundo & Matos e Figueira 1159* (BM); at km 6.4 between Humbe and Catequero, *Sousa 50* (K); Humbe, *Gossweiler 10731* (BM), *Henriques 213* (BM, K); between Cahama & Tchipelongu, *Pearson 2407* (K); at km 20 on the Cahama to Roçadas road, *Borges 334* (K); Chitado, near the Catoni River, *de Menezes & Henriques 88* (K).

Namibia. Ovamboland: Ombepera, *de Winter & Leistner 5499* (K); 12 miles SW of Omafo [Dam] on the road to Ndota Store, *de Winter 3627* (K); near Oshikango, *Rodin 2622, 8962* (K), *de Winter & W. Geiss 7033* (K). Grootfontein District: 4.7 miles E of Otavi on the road to Grootfontein, *de Winter 2861* (K); Simkue [Tsumkwe], 157 miles E of Grootfontein, *Story 6184* (K). Okavanga Native Territory: 6 miles E of Tondoro Mission on the road to Lupala, *de Winter 3964* (K); 35 km W of Andara, *N. Giess 9531* (K); Shitangadimba Camp at Andara Mission Station, *de Winter 4235* (K).

Botswana. Ngamiland: Gaenga Island, *P. A. Smith 1157* (K); Kwebe Hills, *Lugard 38* (K). Nata River, 7 miles from the mouth near Madsiara drift, *Drummond 5290* (K). Near Kanye, ½ mile E of Pharing, *Miller B/516* (K).

Zimbabwe. Matabeleland: Bulawayo, *Eyles 1082, Chubb 321* (BM), *Best 498* (K); Matopo Hills (Park), *Gibbs 261* (BM); near Balla Balla, *Hafstrom & Acocks 1888* (K). Midlands: Gatooma, *Herb. Dept. Agr. S. Rhodesia 1246* (K). North Mashonaland: Darwin District, near the Mkumburu River on the road to Tete, *Phipps 2397* (K); Mkota Reserve, Goromonzi, *Wild 2673* (K); Suskwe [Sutskwe], *Phelps 70* (K). Manicaland: near Umtali, *Fries, Norlindh & Weimarck 2913* (K), *Chase 106* (BM). Victoria Province: Lower Sabi [River], E Bank, Chibuwe, *Wild 2329* (K).

South Africa. Transvaal: Waterpoort turn-off on the Louis Trichardt to Messina road, *Werdermann & Oberdieck 2002* (K); Soutpansberg Mts., about 5 miles above Louis Trichardt, *Rodin 3996* (K); Bandolier Kop, *Burtt Davy 20453, Schlieben 7246, 7281* (K); Duiwelskloof, *Scheepers 1169* (K); Rustenburg, *Galpin 11632* (BM, K); Wonderboom (about 4 miles out of Pretoria), *Moss 3021* (BM), *Phillips 3017* (K); Loskop Dam Nature Reserve, *Mogg 29950* (K). Barberton, *Thode A1579* (K); Kruger National Park, Pretorius Kop area, *van der Schyff 421, 422* (K); Komatipoort-Nelspruit, *Strey 3987* (K). Swaziland: Stegi, Malinda Hills, *Compton 28016* (K). Natal: 5 miles N of Lake Sibayi, *Vahrmeijer & Tolken 284* (K); Itala Nature Reserve, Itala River Valley ca. ½ mile downstream from the warden's house, *Brown & Shapiro 278* (K); Keza Mt. flats, *Strey 9128* (K); Shongweni Dam, *Morris 562* (K); Hlogweni Forest, just S of Tugela River mouth, *Moll 3624* (K); Inanda, *Wood 1148* (K); Hillary, *Coleman s.n.* (K); Isipingo North, *Ward 5256* (K).

Mozambique. Nampula Province: Mutuali, road to Lurio River, 2 km before this river, *Gomes e Sousa 4072* (K). Zambezia: Namagoa, 200 km inland from Quelimane, *Faulkner 2* (BM, K); 9 km from Mocuba, between Mocuba and Maganja da Costa, *Grandvaux Barbosa & Carvalho 20098* (K). Manica e Sofala: between Mandie & Mungari, *Tôrre 3713* (K); Chiou, CICA Experimental Station, *Balsinhas & Macuácua 551* (BM, K); Chupanga, *Le Testu 503* (BM); mouth of the Zambezi, *Kirk s.n.* (K); ascent of Garuso, *Gilliland 1878* (BM, K); Gorongosa, 30 km from the entrance of the national game park toward Villa Paiva de Andrade, *Tôrre & Paiva 9211* (K); between Vila Machado and Vila Pery, *Tôrre 5921* (K). Inhambane: Zavala, *Gomes e Sousa 2051* (K). Maputo: Delagoa Bay, *Monteiro s.n.* (K), *Swynnerton 6514* (BM).

MEDICINAL USES OF PLANTS ON MAURITIUS[1]

LINDA K. SUSSMAN[2]

ABSTRACT

Plant species found on Mauritius are medicinally used in home treatment by laymen and by three types of healers—specialized Creole healers, professional Tamil healers, and folk healers. In this plural medical system, different types of healers are chosen for different types of illnesses. Home treatment and advice from folk healers is selected mainly for common, acute illnesses of short duration that produced little disability. Treatment by professional Tamil herbalists is usually utilized for chronic and recurrent illnesses of long duration that result in slight disability. Specialized Creole healers specialize in treating a limited set of illnesses and are usually consulted for long-term, chronic ailments that produce slight disability. Moreover, herbalists and specialized healers are usually consulted as second or third resorts after biomedical treatment has failed to produce satisfactory results.

RÉSUMÉ

Les espèces de plantes que l'on trouve dans l'île Maurice sont utilisées en médecine par des profanes et par trois sortes de guérisseurs, des créoles spécialisés, des Tamils professionnels et des guérisseurs traditionnels. Dans ce système médical pluraliste, on choisit différents guérisseurs selon la maladie. Les traitements domestiques et les conseils des guérisseurs traditionnels sont selectionnés principalement pour des maladies courantes et graves, de courte durée et qui n'entraînaient qu'une incapacité minime. On utilise en général le traitement des herboristes Tamils professionnels pour des maladies chroniques et périodiques qui causent une légère invalidité. Les guérisseurs créoles spécialisés s'occupent d'un nombre limité de maladies et on les consulte généralement pour des maladies chroniques durables entraînant une invalidité légère. De plus, on consulte les herboristes et les guérisseurs spécialisés en deuxième ou troisième recours quand le traitement biomédical n'a pu donner des résultats satisfaisants.

Mauritius, a small island in the Indian Ocean first permanently settled in the eighteenth century, is a polyethnic society consisting of individuals of African, Indian, French, and Chinese origin. This cultural diversity is reflected in the numerous types of secular and religious healing practitioners found on the island. Secular healers consist of government and private biomedical professionals, homeopathic practitioners, Ayurvedic practitioners, Chinese doctors and acupuncturists, professional Tamil herbalists, folk herbalists, sorcerers, and specialized secular healers (*dimun ki fer passe*). Religious practitioners who may be consulted for health-related problems include Hindu *maraz,* Tamil *poussari,* Buddhist sisters, Mulsim *miadee,* and Christian priests and ministers. Home treatment with herbs, patent medicines, and visits to religious shrines and temples are also healing resources available to Mauritians.

This plural medical system is accompanied by a multicausal medical belief system in which it is thought that illness may be caused by a variety of factors including natural causes such as germs, parasites, infection, and poor diet, and other causes such as sorcery, dead souls, and displeased saints. Accordingly, different types of practitioners are believed to be appropriate for treating different types of illness and no single practitioner is capable of treating all causes (Sussman, 1981). Healing systems involving the ingestion of medicinal plants are all appropriate for the

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treatment of naturally caused illness (*malade Bondieu*).

The medicinal use of plant materials is an integral part of the healing practices of many Mauritian practitioners; and homeopathic, Ayurvedic, and Chinese practitioners make use of a wide variety of imported plant products. However, laymen and two types of healers, specialized secular healers (*dimun ki fer passe*) and professional Tamil herbalists, utilize plant species found on Mauritius for medicinal purposes. They have thus adapted practices originating in other geographic areas to the Mauritian setting, and it is these healing traditions, along with self-treatment, that will be focused on in this paper.

The purpose of this paper is to discuss the extent of the medicinal use of plants found on Mauritius by both laymen and healers and to describe the uses of a selected group of plant species. First I briefly describe the Mauritian healing systems that utilize medicinal plants and then discuss the frequency with which each system is used and the types of illness for which they are usually utilized. Finally, I briefly describe the specific medicinal uses of two groups of plant species, one consisting of the most widely known and used species and the other composed of species indigenous to Mauritius, many of which are unstudied pharmacologically.

Methods

Results are based on a 22-month field study on Mauritius consisting of 1) a survey of healers and their patients and 2) a study of the health-seeking behavior of 32 households in the rural southwest. The households were composed of 198 individuals, comprising 8% of the total population of two adjacent villages. Data were collected on 456 illness episodes experienced during the study period. Members of each household were also questioned about their knowledge of the medicinal uses of a list of 110 plant species.

In this study I was thus able not only to construct a list of the medicinal uses of plant species used by healing specialists but also to: a) collect data on the general knowledge of the lay population in the rural southwest about the medicinal uses of plants and on attitudes about herbal treatment, b) observe the actual use of plant remedies for illness episodes experienced by respondents during the study, and c) determine the frequency with which treatment by medicinal plants was utilized.

Healing Systems

Specialized Secular Healers (*Dimun ki fer passe*)

Specialized secular healers utilize herbal remedies, "passes," "marking" (see below), and prayers to heal specific types of illness. They are numerous and may be found in most towns and villages throughout the island. The overwhelming majority are elderly Roman Catholic Creoles, although there are also some Christianized Tamil healers of this type. This tradition may represent a blend of European, and perhaps Malagasy and African, herbalism and Christian practices such as the laying on of hands. It is similar in many respects to the herbalist tradition among small-scale white farmers on the neighboring island of Réunion (Benoist, 1980) and may be of similar origin.

The illnesses treated by this type of healer are quite specific. They consist mainly of sprains and pulled muscles (*foulire*), skin rashes and infections (*gratelles* and *dartes*), aches and pains resulting from rheumatism or arthritis (*doulère*), backaches associated with kidney ailments (*les-reins*), headaches (*gayn soley*), stone fish stings (*lafo*), "coldness" (*fraisère*), and *tambave,* a childhood ailment widely recognized on the Mascarenes and Madagascar.

The term *tambave* is derived from the Malagasy *tambavy,* which denotes both a childhood ailment inherited from the mother and the herbal remedy for it (Richardson, 1885; Abinal & Malzac, 1970).

Fraisère, tambave, gayn soley, and *dartes* denote syndromes that are recognized by the majority of Mauritians and believed by most to be curable only by specialized secular healers. *Fraisère* is characterized by chronic coughing, sneezing, or respiratory congestion. It is believed to be caused by coldness that is trapped in either the head or chest as a result of the absorption of cold water or exposure to cold, damp weather.

Tambave is characterized by chronic skin eruptions on the bodies of infants and small children, especially around the head and face, and may be accompanied by gastrointestinal disorders. Biomedical physicians do not regard it as a unitary syndrome. Mauritians, however, view *tambave* as an illness syndrome to which all children are susceptible. They believe that it results from unclean blood, with the skin eruptions and/or diarrhea developing in order to release poisons or impurities that are in the blood. The poisons

originally enter the body via food eaten by either the child or, more commonly, the mother during pregnancy or nursing. Measures often taken by parents to prevent the occurrence of *tambave* consist of "marking" (see below) by a healer, along with the use of herbal remedies. It is believed that it is better to rid the child of blood impurities before they become strong enough to manifest themselves in the form of symptoms.

The major symptom of *gayn soley* (literally, "to have sun") is a chronic or recurrent headache. It is believed to be caused by heat or sun trapped in the head as a result of long exposure to the sun. *Dartes* refers to a skin rash distinct from scabies. It is also believed to be caused by impurities in the blood and is treated by marking and herbal baths.

All four of the "folk illnesses" described above have a common etiological pattern and logic of treatment. There is a foreign irritant, either an impurity, heat, or cold, lodged somewhere in the body that causes the symptoms. The aim of treatment by specialized healers is to rid the body of the irritant, thus effecting a permanent cure. The other biomedically recognized ailments treated by these healers—sprains (*foulire*), aches and pains resulting from rheumatism or arthritis (*doulère*), backaches associated with kidney ailments (*lesreins*), and stonefish stings (*lafo*)—also share this feature with the other four folk illnesses and are all associated with either pain or poisons that must be drawn out (*tiré*) by a healer or herbal remedy. While it is recognized that biomedicine may temporarily relieve the symptoms of most of these ailments, it is generally believed that symptoms will recur until their underlying causes have been removed by a specialized healer.

Treatment usually consists of either "marking" or performing "passes." In the former, the healer "marks" the affected area with his or her hand or foot or with a needle or the root of *Vetiveria zizanoides*. A specific number of crosses are traced on the area while an incantation is whispered. This is the usual method of treating sprains, *tambave*, and various other skin ailments. On the other hand, coughs, allergies, chronic bronchitis (all of which may be *fraisère*) and pains associated with rheumatism and arthritis (*doulère*) are drawn out (*tiré*) by performing "passes" in the air in the form of crosses around the affected area with a lit candle and flowers. Simultaneously the healer places one hand on the patient's head and recites an incantation. The healer may then also trace crosses with his/her hands on the affected area while continuing to recite the incantation. One healer explained that the candle provides light for God to see, while the flowers provide a pleasant perfume for God to smell. Both marking and passes are supposed to be performed three days in a row. Treatment by marking and passes is usually supplemented by herbal remedies that the patient is to ingest or bathe in at home. The healer may in some cases suggest dietary changes or restrictions.

Treatment procedures are either passed down within families or learned through apprenticeships, and the actual incantations and contents of herbal remedies are secret. Most of the healers obtained their knowledge from parents, parents-in-law, or spouses. Of the five healers interviewed, three indicated that they will pass on their knowledge to one of their children.

Healers of this type usually charge no fees but may ask for small donations (5 rupees = U.S. $0.65) to cover the cost of herbs, candles, and other materials. Most practice part-time or are "on call" and see patients whenever they are called upon. Some may see only one or two patients per week, while others may be consulted by up to 10 to 20 per day.

PROFESSIONAL HERBALISTS
(*Marsand latisane, Herboriste*)

At least three full-time professional herbalists maintain stalls in urban markets. They are all middle-aged, Indo-Mauritian men of Tamil origin and represent the third generation of herbalists on Mauritius in their families. Their grandfathers had been herbalists in South India before immigrating to Mauritius, and the tradition has been passed down from father to son. I interviewed two of the three herbalists and it appears as if their knowledge may be lost within the next few decades. One is training his son but does not know if he will follow this profession; the other has no children or apprentices.

The herbalists utilize approximately 150–200 different plant species (Sussman, 1980, in prep., for a description of approximately one hundred of these). Although the pharmacopeia of the grandfathers of the herbalists must have been largely of Tamil origin, it is clear that today it consists of a mixture of Tamil, European, and indigenous Mauritian components. The plants utilized consist of indigenous, exotic, and cultivated species. Herbalists buy some of these from

plant collectors. They also collect wild plants and cultivate others in their gardens. Approximately 25% of the plant species utilized are indigenous, including some endemic to Mauritius. Most of these would not have been known to the South Indian immigrants, and their use as medicinal plants must have been developed on Mauritius. Over the three generations, new plant species have therefore been added to or substituted for the original pharmacopeia of the Tamil herbalists. Moreover, today the herbalists read literature on European herbalism and frequently incorporate into their pharmacopeia those species that are available or can be cultivated in their gardens.

Most of the remedies prepared by the herbalists consist of a combination of several plant species, the number in a single remedy ranging from one to eleven (Sussman, 1980). The remedy is sold in the form of crushed dried plant parts. The dried mixture is then prepared for use by the patient, who follows the herbalist's directions. The usual way of preparing remedies to be taken internally is to make either a decoction by boiling the mixture in water 15–20 minutes or an infusion by steeping it in hot water. The patient is instructed to drink a certain number of cups of the infusion or decoction per day for a particular number of days. For remedies to be used externally, the plants are boiled together in water and the patient either bathes in the solution or washes the affected area with it for a certain number of days. Patients are instructed to prepare each dosage individually at the time it is utilized and not to prepare a batch ahead of time.

The herbalists are consulted for a wide variety of ailments and list 34 illnesses or symptoms on their business cards as being treatable by herbs. The two herbalists I observed each saw approximately 30–40 clients per day, many of whom come to buy remedies for illnesses that have been diagnosed by biomedical physicians. The determination of appropriate herbal mixtures is based upon questioning the patient about his symptoms and, in some cases, diet and previous diagnoses by biomedical physicians. The age and sex of the patient are also considered in determining appropriate remedies and doses. In addition to herbal mixtures, the herbalists may also suggest that the patient change his dietary habits and/or refrain from eating particular food items. They are well aware of the limitations of their treatment and may refer clients to biomedical physicians either for diagnosis, if the symptoms are not clearcut, or for treatment, if the illness is not conducive to treatment by plant remedies (Desvaux, 1979). They also inform patients with particular ailments (e.g., chronic disorders such as rheumatism or diabetes) that the remedy cannot cure the illness but will only temporarily alleviate or control the symptoms.

The herbalists do not perceive themselves as being in direct competition with biomedical physicians. In fact, as indicated above, many of their clients seek diagnoses from governmentally supported medical facilities and then buy remedies for their illnesses from the herbalists. Natural herbal remedies are frequently preferred by patients over biomedical treatment for chronic ailments such as hypertension, diabetes, and rheumatism or are alternated with biomedical medication to "give the body a rest from the medicine."

Moreover, medications from pharmacies are expensive, while herbal remedies are relatively inexpensive. During 27.5 hours of observation in 1977 and 1979–1980, the average fee charged by the herbalists was 2.74 rupees ($0.45), with most prices ranging between 1.00 and 3.00 rupees ($0.17 to $0.50). This is considerably less than would be charged for most medication at either a biomedical or Chinese pharmacy. The herbalists are thus probably more in competition with pharmacists than with physicians. Both of the herbalists I observed are strongly motivated to help people and feel that one of their greatest contributions is their ability to offer inexpensive health care to the population.

LAY FOLK HERBALISTS

Folk herbalists consist mainly of middle-aged or elderly women who are well versed in the use of medicinal plants and who may be the descendants of a type of local herbalist-healer that no longer exists. Until the twentieth century there were few doctors and biomedical facilities, especially in the rural areas. Moreover, although the island is quite small and there were roads and some railroads connecting major towns and cities in the nineteenth century (Pike, 1873), transportation from rural areas to facilities in the major cities was slow. This was a major reason for requiring sugar estates, which were mainly in rural areas, to maintain dispensaries for their workers. It is probable that until the increase in the number of hospitals and dispensaries and the improvement of public transportation and roads,

health problems were treated at home with herbs and the use of local herbalist-healers.

In the 1860s, Pike noted the abundance of dried herbs sold in the central market in Port Louis, the capital city: "There is scarcely a leaf or bark of indigenous or exotic plant or tree that is not used by Creole or Indian for some ailment. They have the most profound faith in herb teas or tisanes . . ." (1873: 66). Pike does not describe the herbalists themselves. It is thus unclear whether the herb sellers in the Port Louis market were the ancestors of the professional Tamil herbalists there today or whether they represented a different, perhaps Creole, group of herbalists. If the Tamil tradition on Mauritius dates back only two generations, as the herbalists report, it may not have begun until the last decade of the nineteenth century.

Of the residents in the southwest whom I questioned about medical practices in the past, 96% (N = 25) stated that the grandparents usually relied upon home herbal remedies and local practitioners who used plant remedies and other treatment techniques such as "marking." They believe that in the past laymen had much greater knowledge about herbal remedies than today.

According to most informants, "folk herbalists" are still quite numerous but declining in number because their knowledge is not being passed on to the younger generations. I interviewed two women who fall into this category, a Creole/Chinese and a Creole. Both live in the Port Louis area and are 55–65 years old. They obtained their knowledge from Creole parents and/or grandparents who, they say, had been professional "healers." One learned from her grandmother who had been a specialist in children's illnesses and who utilized both herbal remedies and "marking." The other learned from her maternal grandfather and mother; her grandfather had been a "healer."

These women collect medicinal plants in the forests and countryside and also grow some species in their gardens. They are well known in their communities and are consulted for a variety of ailments. They do not charge for their services or advice. They treat only ailments that are "naturally" caused, most of which are common, minor ailments. Treatment is based upon the symptoms reported by the patient and usually consists of one or more herbs boiled together in water. One of the practitioners also utilizes ingredients that can be purchased at local general stores, such as epsom salts, cod liver oil, mustard, and alcohol. Both stated that they would refer patients to biomedical physicians for serious ailments or those for which they did not know a cure. They related remedies to me for the following illnesses or complaints: amenorrhea (usually pregnancy requiring an abortifacient), anemia, bruises, burns, colic, constipation, cough, diabetes, diarrhea, earache, edema, fever, gas, headache, heart palpitations, hypertension, hemorrhoids, hernia, indigestion, influenza, insomnia, jaundice, kidney ailments, liver disorders, menstrual cramps, nerves, pimples, respiratory congestion, scabies, skin rashes, sprains, *tambave,* ulcers, vomiting, and worms.

TABLE 1. Mean percentage of plant species and medicinal uses known by respondents on each of three plants lists.

	Species Known		Medicinal Uses Known		
	Mean %	s.d.	Mean %	s.d.	N
List #1	49.4	16.8	27.1	14.9	38
List #2	62.4	17.2	43.9	20.5	35
List #3	72.4	24.1	45.6	33.4	26

HOME TREATMENT BY LAYMEN

Laymen also resort to home treatment with medicinal plants, especially for common, minor ailments. Some individuals maintained gardens stocked with a variety of medicinal plants. Some plant species are simply collected along the roadside or in the countryside while others are bought from professional Tamil herbalists.

Although all of the village residents in this study believed that herbal treatment was appropriate for some naturally caused illnesses, there was considerable individual variation in their propensity to utilize such treatment for themselves or members of their family (Sussman, 1983). Some felt that it was more convenient to obtain tablets or syrups from the local government dispensary. Many, however, believed that such medication was too strong and "shocked" the body, while herbal treatment was effective and produced no side effects. A commonly expressed belief was that if one had to take medication for a chronic illness such as hypertension or rheumatism, it was desirable to periodically substitute an herbal remedy for the medication in order to give the body a rest from the medication.

TABLE 2. Knowledge of medicinal plants by members of different age groups.

	Mean Score (%)		
	Under 30	30 or older	t
Know plant species			
List #1	34.9	55.3	4.0[a]
List #2	50.1	66.4	2.5[b]
List #3	71.6	72.6	0.1
Know medicinal use			
List #1	18.5	30.6	2.4[b]
List #2	31.1	48.3	2.3[b,c]
List #3	44.4	45.9	0.1

[a] $P \leq 0.001$.
[b] $P \leq 0.05$.
[c] Regression analysis by age category ($\leq$29, 30–39, 40–54, $\geq$55) also significant at the 0.05 level.

A sample of village residents was asked whether they could recognize 110 plant species (covered in three separate interviews) and whether they knew of their medicinal uses. Both the familiarity with plant species and the knowledge of their medicinal uses varied substantially from household to household, as can be seen from the high standard deviations shown in Table 1. Respondents consisted of both Creoles of African origin and Indo-Mauritians of Indian origin, but there were no significant ethnic differences in the extent of knowledge of medicinal plants.

The age of the respondent, however, was significantly related to both the familiarity with plant species and their medicinal uses (Table 2). Individuals under 30 years of age were significantly less knowledgeable about the plant species on two of the three lists. In general, species on list 3 (Tables 1, 2) were the most commonly known and widespread in the southwest, whereas many on lists 1 and 2 were not found in the region. Respondents over 30 thus tended to be familiar with a wider variety of plant species and their medicinal uses and with a greater number that were not found in the immediate vicinity of the village.

It is possible that the effect seen here indicates simply that as one grows older one accumulates more knowledge, and thus in another ten years individuals currently under 30 will have accumulated greater knowledge of medicinal plants. However, regressions run on these data indicate that, with one exception (list 2), there is not a linear relationship between either absolute age or age group (<29, 30–39, 40–54, 55+) and knowledge of medicinal plants. Rather, there appears to be a significant difference between individuals under 30 and those in the older age groups. This might well reflect an actual cohort effect indicating that individuals under 30 are not learning as much about the medicinal uses of plants or about the plant species in their environment in general.

If this is the case, lay knowledge of the medicinal uses of plants may be rapidly reduced during the next few decades, since this knowledge is usually passed down from mother to daughter. In fact, data collected on the knowledge of both mothers and daughters in eight households indicate that daughters know less than their mothers about medicinal plants. They knew, on the average, 20% fewer plant species on the lists than their mothers ($P < 0.05$) and knew about the medicinal uses of 15% fewer species ($P = 0.15$) (Table 3). According to these data, an average of 33% of the mothers' knowledge was not passed on to the daughters. Although a survey clearly needs to be conducted on a larger sample of households, if we assume that the average loss of knowledge per generation is approximately 33%, in just three generations only one-fifth of the knowledge of current mothers will be preserved. The range of variation, however, was considerable, with the loss of knowledge of the medicinal uses of plants ranging from 6% to 88%. Therefore, in actuality this knowledge would be

TABLE 3. Comparison of knowledge of mothers and daughters.

	Average Scores/Household (N = 8)			
	Mothers	Daughters	Average Difference	Average Loss
% Species known[a]	60.8	41.2	−19.6	32.7
% Medicinal uses known[b]	41.3	26.6	−14.7	32.3

[a] $t = 2.3$, $P = 0.04$.
[b] $t = 1.5$, $P = 0.15$.

TABLE 4. Medicinal plants known by at least half of the respondents ranked from most to least known.

Plant Species	Creole Name	% Who Knew the Remedy	Illness
Cymbopogon citratus Stapf	Citronelle	100	Cough
Eupatorium ayapana Vent.	Ayapana	97	Vomiting
Mentha sp.	Lamenthe	97	Indigestion
Cocos nucifera L.	Coco	85	Indigestion
Pongamia pinnata (L.) Merr.	Coquelisse	84	Whooping cough
Litsea glutinosa C. B. Robinson	Bois d'oiseau	84	Indigestion
Mimosa pudica L.	Sensisive	81	Nerves, children
Ageratum conyzoides L.	Herbe de bouc	79	Gas/indigestion
Quisqualis indica L.	Badamier sauvage	78	Worms
Chamaemelum nobile (L.) All.	Camomille	77	Vomiting, infants
Ocimum basilicum L.	Tulsi	76	Indigestion
Bryophyllum pinnatum Kurz	Sulfaf	72	Rheumatism
Centella asiatica L.	Boileau	71	Skin rash
Cassia occidentalis L.	Casse piante	69	Fever
Prunus persica (L.) Batsch.	Feuilles peche	60	Worms
Euphorbia hirta L.	Jean Robert	56	Diarrhea
Catharanthus roseus	Sapponaire blanc	54	Indigestion
Acalypha indica L.	Herbe chatte	51	Skin rash
Cassia alata L.	Kattrepeng	49	Hypertension

lost very rapidly in some households and preserved over many generations in others.

The most widely known herbal remedies are for common, relatively minor ailments. From the most to least known, these include coughs, vomiting, indigestion, childhood convulsions or nervousness, worms, rheumatism, skin rashes, fever, diarrhea, and hypertension (Table 4). Over 80% of the respondents knew at least one home herbal remedy for minor coughs and colds, vomiting, indigestion, whooping cough, and childhood nerves (*crises,* usually associated with teething). Moreover, most laymen tended to possess knowledge of a rather small number but specific set of medicinal plants; 19 of the plant species on the lists were known by at least 49% of the respondents.

Frequency of Herbal Treatment and Illnesses Most Commonly Treated

I noted earlier that there was a plural medical system on Mauritius in which there were numerous types of healers from which to choose. Here I shall briefly attempt to portray the use of herbal treatment within this context of medical pluralism.

In general, during an illness episode a patient chooses a practitioner or type of treatment depending on the illness itself and on its characteristics and response to previous treatments. During the study of village residents, most of the illness episodes (N = 456) were acute, of short duration, and involved little disability. Most of the illnesses were brought to the attention of a single healing specialist. In cases for which more than one practitioner was consulted, practitioners were usually utilized serially; it was extremely rare for a patient to use two different kinds of treatment for the same illness simultaneously.

Treatment at the local government dispensary (39.3% of the choices), home treatment (23.1%), and no treatment (16.1%) accounted for most of the treatment choices for these illness episodes (Table 5). (The government medical system provides treatment free of charge at both local dispensaries and regional hospitals, and these services are highly utilized by the population.) Although it had been used at some time in the past by at least half of the heads of household, herbal treatment, either at home or by professional Tamil herbalists or specialized healers, was used relatively infrequently during the village study and accounted for less than one in ten treatment choices. Moreover, while home treatment tended to be used with equal frequency at all levels of resort, herbalists and specialized healers tended to be consulted after other treatments, usually biomedicine, had been found to be unsuccessful.

TABLE 5. Treatment choices by members of each ethnic group at all levels of resort.

Type of Practitioner	% Times Chosen[a]	% Illness Episodes[b]
Government facility	39.3	47.6
Private doctor/nurse	7.1	8.8
Pharmacist	8.1	10.1
Herbalist	0.4	0.4
Traditional midwife	0.4	0.4
Home treatment, all forms	23.1	27.4
Home treatment w/herbs	7.3	9.0
Home treatment w/biomedicine	9.6	11.4
Home treatment w/other	6.2	7.7
Specialized healer	1.1	1.3
Catholic priest	0.2	0.2
Hindu *maraz*	0.4	0.4
Sorcerer	0.2	0.2
No treatment	16.1	19.5
Unknown, no response	3.9	4.8
N	565	456

[a] This represents the tabulation of all healing resources utilized at all levels of resort, including those used twice, but at different levels of resort, for a single illness episode.

[b] The sum of this column is greater than 100% because more than one practitioner was consulted for some illness episodes.

Home treatment was chosen mainly for acute illnesses of short duration (4–7 days) that produced little disability (Table 6). Treatment by professional Tamil herbalists was associated with chronic and recurrent illnesses of long duration (over three weeks) that resulted in slight disability, and treatment by specialized healers was associated with long-term chronic illnesses producing slight disability.

Biomedicine was chosen for acute illnesses of short duration producing little disability and was also the most commonly preferred treatment for uncommon, serious illnesses (Sussman, 1983). Religious specialists and sorcerers were usually consulted for long-term chronic or recurrent illnesses with at least slight disability associated with them and which had not responded well to "natural" biomedical or herbal treatment.

Members of both sexes and of all ethnic and age groups utilized both specialized healers and Tamil herbalists (Table 7). Specialized healers were consulted most frequently for skin ailments and respiratory problems. While some patients used these healers as a first resource, especially for *tambave*, sprains, and pulled muscles, 41% of the patients observed had tried other types of practitioners before consulting the healer. Three-quarters of the patients complaining of chronic coughs and rheumatism had previously consulted biomedical physicians. In two of six such cases among village residents, previous treatment by biomedicine had failed to produce a cure, while it was believed by the patients that the specialized healer had either effected a cure or at least improved the condition.

Tamil herbalists were most frequently consulted for gastrointestinal disorders, skin ailments (including *tambave*), liver problems, diabetes, heart palpitations and nerves, fever, amenorrhea (usually pregnancy requiring an abortifacient), kidney disorders, urinary calculi, and respiratory ailments. In Mauritian Creole, complaints of "liver problems" (*le foie*) may refer to either serious diseases of the liver that have been diagnosed by physicians or to feelings of general gastrointestinal discomfort—nausea, constipation, indigestion, etc. Patients were questioned in detail about their symptoms whenever possible. However, the number of cases of "liver" complaints may be overrepresented and the number of gastrointestinal disorders underrepresented as a result of this ambiguity in ter-

TABLE 6. Median characteristics of the illnesses brought to each type of practitioner.

Type of Practitioner	Type of Illness	Disability	Duration
No treatment	Acute	None	3 days
Home treatment	Acute	None	4–7 days
Pharmacist	Acute	None	4–15 days
Government facility	Acute	Slight	2–3 weeks
Sorcerer	Acute and chronic	Major	2–3 weeks
Private doctor	Chronic and acute	Slight	Over 3 weeks
Herbalist	Chronic/recurrent	Slight	Over 3 weeks
Specialized healer	Chronic	Slight	Over 3 weeks
Catholic priest	Chronic	Slight	Over 3 weeks
Hindu priest	Chronic/recurrent	Major	Over 3 weeks

minology. Another popular remedy was an herbal mixture (mainly a diuretic) for losing weight.

Home treatment by herbs was mainly utilized for gastrointestinal complaints, respiratory ailments, skin rashes, and rheumatism. Home treatment was used by both Creoles and Indo-Mauritians and by both males and females. Almost one-third of the patients treated at home were children under the age of 11 (32%). Most of the home treatment was for acute illnesses (66%) of less than one week's duration (50%), resulting in no disability or reduction in daily activities (66%). The great majority of patients treated at home with herbal remedies were either cured or better (88%) following the treatment.

Most Commonly Utilized Plant Species

The most commonly used species for home treatment are not indigenous to Mauritius. They consist of commercially and home-cultivated species such as *Cocos nucifera* (coconut), *Prunus persica* (peach), *Mentha* sp. (mint), *Cymbopogon citratus* (lemon grass), *Eupatorium ayapana, Cassia alata*; seeds that are sold in the local general stores (*Linum usitatissumum, Hordeum vulgare, Salvia coccinea*); and species that grow wild along roadsides and in forests or savannahs (*Litsea glutinosa, Quisqualis indica, Cassia occidentalis, Mimosa pudica, Bryophyllum pinnatum, Centella asiatica, Acalypha indica,* and *Ageratum conyzoides*) (Table 8A).

On the other hand, many of the most important species utilized by healing specialists are indigenous to Mauritius (or Madagascar, as in the case of *Ravenala madagascariensis*) (Table 8B). Of special note because of their unstudied status and/or claims concerning their effectiveness are the following species: *Faujasia flexuosa,* an endemic species used in the treatment of diabetes; *Psiadia trinervia,* another endemic used for asthma and respiratory congestion; *Elaeodendron orientale,* used for hypertension; *Selaginella* sp., used as a sedative; *Paederia tomentosa,* a liana indigenous to Asia used in the treatment of stomach ulcers; and the bark of *Erythroxylum laurifolium,* used as a diuretic and treatment for urinary calculi. *Aphloia theiformis* is also noteworthy because it is included in herbal mixtures used to treat a wide variety of illnesses—diabetes, kidney ailments, urinary calculi, liver disorders, jaundice, and anemia.

As noted earlier, many of the clients of professional herbalists had had their illnesses diagnosed by biomedical physicians. Furthermore, many of those with chronic ailments, such as diabetes and hypertension, continued to consult their physicians while being treated by the herbalists to determine whether their illnesses were being adequately controlled by the herbal medicines. The patients with diabetes whom I interviewed confirmed that the herbal remedies had controlled their diabetes and that they required no additional medication. Some had been taking

Table 7. Illnesses for which medicinal plants were utilized.

	Percentage of Patients Treated		
	Specialized Healer (N = 32)	Tamil Herbalist (N = 161)	Home Treatment (N = 41)
Illness/Symptom			
Respiratory	50.0	5.6	14.6
Skin rash	31.3	11.2	7.3
Sprains	9.4	—	—
Rheumatism	6.3	1.2	7.3
Backache	3.1	—	—
Gastrointestinal	—	11.2	43.9
"Liver"	—	11.2	—
Diabetes	—	9.9	—
Fever	—	8.7	2.4
Palpitations, nerves	—	8.7	—
Weight loss	—	8.1	—
Amenorrhea	—	6.2	—
Kidney/urinary tract	—	5.6	—
Hypertension	—	1.2	2.4
Anemia	—	1.2	—
Dizziness	—	—	4.9
Other	—	9.9	17.1
Ethnic group			
Creole	56.3	41.6	63.4
Indo-Mauritian	40.6	42.9	36.6
Other	3.1	15.6	—
Sex			
Male	41.9	46.0	41.5
Female	58.1	54.0	58.5
Age			
0–10	22.6	6.3	31.7
11–19	19.4	4.4	7.3
20–29	19.4	22.5	12.2
30–39	12.9	16.3	7.3
40–49	16.1	23.8	19.5
50–59	—	15.0	7.3
≥60	9.7	11.9	14.6

TABLE 8. A selected group of medicinally used plant species.[a]

Illness/Symptom	Genus/Species	Family
A. Most Commonly Known and Used		
Indigestion	*Mentha* sp.	Lamiaceae
	Cocos nucifera L. (root)	Arecaceae
	Litsea glutinosa C. B. Robinson	Lauraceae
	Salvia coccinea (seeds)	Labiatae
	Linum usitatissumum L. (seeds)	Linaceae
Amebiasis	*Hordeum vulgare* L. (seeds)	Poaceae
Parasites	*Ageratum conyzoides* L.	Asteraceae
	Quisqualis indica L. (seeds)	Combretaceae
Cough	*Prunus persica* (L.) Batsch.	Rosaceae
Fever	*Cymbopogon citratus* Stapf	Poaceae
Vomiting	*Cassia occidentalis* L. (root)	Fabaceae
Nerves/palpitations	*Eupatorium ayapana* Vent.	Asteraceae
Asthma	*Mimosa pudica* L.	Fabaceae
Hypertension	*Cassia occidentalis* L. (seeds)	Fabaceae
Rheumatism	*Cassia alata* L.	Fabaceae
Skin rash	*Bryophyllum pinnatum* Kurz (bath)	Crassulaceae
	Centella asiatica L. (bath)	Apiaceae
	Acalypha indica L. (bath)	Euphorbiaceae
B. Species Widely Used by Specialists (Indigenous unless noted)		
Diabetes	*Faujasia flexuosa* Benth. & Hook f.	Asteraceae
	Bruguieria gymnorhiza Lam./*Rhizophora mucronata* Lam. (root)	Rhizophoraceae
	Ravenala madagascariensis J. F. Gmel. (heart)[b]	Strelitziaceae
Sinusitis	*Aphloia theiformis* Benn.	Flacourtiaceae
Respiratory problems	*Terminalia angustifolia* Jacq. (bark)	Combretaceae
	Psiadia trinervia Willd.	Asteraceae
Dysentery	*Plectranthus madagascariensis*	Lamiaceae
	Terminalia angustifolia Jacq. (bark)	Combretaceae
Hypertension	*Tristemma virusanum* Juss.	Melastomataceae
	Elaeodendron orientale Jacq.	Celastraceae
	Bruguieria gymnorhiza Lam./*Rhizophora mucronata* Lam. (root)	Rhizophoraceae
Palpitations/nerves	*Selaginella* sp.	Selaginellaceae
	Potamogeton chamissoi A. Benn.	Potamogetonaceae
Ulcers/indigestion	*Paederia tomentosa* Blume[c]	Rubiaceae
Diuretic/urinary calculi	*Erythroxylum laurifolium* Lam. (bark)	Erythroxylaceae
	Aphloia theiformis Benn.	Flacourtiaceae
Liver/jaundice/anemia	*Aphloia theiformis* Benn.	Flacourtiaceae
	Microsorium polycarpon	Polypodiaceae

[a] Unless otherwise stated, the leaves of the plant are used medicinally.
[b] Indigenous to Madagascar.
[c] Indigenous to Asia.

herbal mixtures for many years. Most had been taking *Faujasia flexuosa* alone; a few had been taking a mixture of *Faujasia flexuosa, Ravenala madagascariensis, Aphloia theiformis,* and mangrove (*Bruguieria gymnorhiza* or *Rhizophora mucronata*—these used interchangeably). Likewise, those patients with hypertension stated that *Cassia alata* alone, *Elaeodendron orientale* alone, or both, in combination with mangrove, had successfully controlled their high blood pressure.

Psiadia trinervia was claimed by both specialists and patients to be very effective for asthma and other respiratory complaints. *Paederia tomentosa* was said to be extremely effective in treating stomach ulcers, even those for which biomedical physicians had recommended sur-

gery. Lastly, the bark of *Erythroxylum laurifolium* was claimed to be an effective diuretic, causing urinary calculi to be dissolved or passed without any biomedical treatment.

Conclusion

With the increasing availability of biomedical care, especially by free government facilities, the medicinal use of plants is decreasing. In fact, during the village study of treatment-seeking for 456 illness episodes, treatment by medicinal plants accounted for only one in ten treatment choices. Accompanying this is the reduction in lay knowledge about not only the medicinal uses of plants but also about the identity of plants in the environment. Furthermore, there are currently only three full-time professional herbalists on the island and it is unclear how many of the next generation will remain to carry on this tradition. These herbalists utilize many indigenous plant species and it is extremely important that the pharmacological properties of these species be investigated as soon as possible. Moreover, these species are frequently used in combination with each other and it is thus important to begin studying their pharmacological properties while the extensive knowledge and experience of the herbalists are still available to us.

Furthermore, many of the indigenous species are becoming increasingly rare. Mauritius is a tiny island of 720 square miles with little remaining native forest. Wild members of the indigenous species are being exploited for their medicinal value. And, although in recent decades the use of medicinal plants has presumably been supplanted to a great extent by the use of biomedicine, the population of Mauritius is extremely dense (over 1,200 per square mile) and has doubled in the past 30 years. Thus, even given the relatively low level of use of medicinal plants, these plant species appear unable to reproduce themselves at a rapid enough rate. Herbalists have commented that it is becoming increasingly difficult to find some of the indigenous species because their numbers are rapidly decreasing. For example, *Bois fier* (*Bakerella hoyifolia*) was once used as a remedy (Daruty, 1911). Today, however, there are very few (under 10) known individuals of this species remaining (Lorence, pers. comm.). Even *Erythroxylon laurifolium, Faujasia flexuosa, Psiadia trinervia,* and *Asplenium nidus*—widely used remedies for urinary calculi, diabetes, asthma, bronchitis, and liver disorders—are becoming more and more difficult to find.

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SOME USEFUL PLANTS IN EAST-CENTRAL AFRICA: A CROSS-CULTURAL ETHNOBOTANICAL SURVEY

GLORIA WAITE[1]

ABSTRACT

This study presents multidisciplinary information on several plant species that are used for identical medicinal and dietary purposes in eastern Zambia and south-central Tanzania. Some of these species also share common names. The first part of the paper discusses the historical significance of these shared cultural features. It then surveys the biochemical literature on these species or members of the same genus for possible scientific support for their applications.

RÉSUMÉ

Dans cette étude sont présentées des données pluridisciplinaires concernant plusieurs espèces de plantes qui sont utilisées à des fins médicinales ou alimentaires identiques en Zambie orientale et dans le centre-sud de la Tanzanie. Certaines des ces espèces peuvent même avoir des noms en commun. L'auteur discute d'abord de l'importance historique de ces traits culturels semblables puis étudie la littérature biochimique sur ces espèces ou les membres du même genre en vue d'un soutien scientifique possible pour leurs applications.

This paper is derived from a larger, nonbotanical study the author carried out in 1978–1979 among villagers and herbalists in several different agricultural societies in eastern Zambia and south-central Tanzania (Waite, 1981). As part of that research, mounted herbarium specimens were used to collect original cultural data on 38 plant species (Table 1). That material has been compared with the cultural data recorded for these species throughout east-central Africa (Binns & Logah, 1971; Coates Palgrave, 1977; Fanshawe, 1971; Gelfand et al., 1985; Haerdi, 1964; Harvey & Armitage, 1961; Hora & Greenway, 1940; Jansen & Mendes, 1982; Reis & Lipp, 1982; Tanner, 1951; Watt & Breyer-Brandwijk, 1962; White, 1962; Williamson, 1955).

Among the results of this cross-cultural study are indications that 11 of the 38 species are used identically in eastern Zambia and south-central Tanzania, either as medicines or as foods, and one is used as a fish poison. Of the 11 species with shared uses, seven are used medicinally. Several medicinal applications are reported for these seven species among the societies in eastern Zambia and south-central Tanzania. However, Table 2 includes only those applications for the species that are shared by societies in the two areas—sometimes, but not generally, by only one society in each area.

The applications for these species (Table 2) could have been independently conceived in the two areas. Some may even be of older use in one area than in the other. It is more likely, however, that these specific applications arose at a time when the societies in the two areas were still relatively undifferentiated and probably not in their present locations but somewhere in the general vicinity. Plant knowledge is generally passed from one generation to another, from older people to younger ones. This does not preclude later acquisition of plant knowledge from others. Some herbalists even receive knowledge of plant applications through inspiration while sleeping. But most plant knowledge is acquired through apprenticeship, generally to an older family member. Therefore the shared applications listed in Table 2 are probably derived from a time when the societies in the two areas were still a common people, before the weight of the centuries and the practice of shifting cultivation added to their differentiation.

Further support for the possible antiquity of the shared applications can be found in the names for these species. Four of these seven species are called by cognate names in the two areas (Table 3). The names in Table 3 are only representative of the names used in the two areas for these species, unless otherwise indicated. Some of these

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TABLE 1. The original 38 species used in this study.

Species	Family
Afromosia angolensis	Papilionaceae
Afzelia cuanensis	Fabaceae
Albizia versicolor	Mimosaceae
Annona chrysophylla	Annonaceae
Cissus integrifolia	Ampelidaceae
Crossopteryx febrifuga	Rubiaceae
Dialiopsis africana	Sapindaceae
Dichrostachys cinerea	Mimosaceae
Diospyros kirkiana	Ebenaceae
Diospyros mespiliformis	Ebenaceae
Diplorhynchus condylocarpon	Apocynaceae
Faurea saligna	Proteaceae
Grewia bicolor	Tiliaceae
Jasminum fluminense	Oleaceae
Kigelia africana var. *aethiopica*	Bignoniaceae
Kirkia acuminata	Simarubaceae
Markhamia acuminata	Bignoniaceae
Markhamia obtusifolia	Bignoniaceae
Maytenus senegalensis	Celastraceae
Ozoroa reticulata (syn. *Heeria*)	Anacardiaceae
Piliostigma thonningii (syn. *Bauhinia*)	Fabaceae
Pseudolachnostylis maprouneifolia	Euphorbiaceae
Rauwolfia caffra	Apocynaceae
Rothmannia fischerii	Rubiaceae
Securidaca longipedunculata	Polygalaceae
Sesamum angolense	Pedaliaceae
Solanum nigrum	Solanaceae
Swartzia madagascariensis	Fabaceae
Syzygium condatum	Myrtaceae
Syzygium guineensis	Myrtaceae
Trichilia emetica	Meliaceae
Uapaca kirkiana	Euphorbiaceae
Uapaca nitida	Euphorbiaceae
Vitex doniana	Verbenaceae
Xeromphis obovata (syn. *Randia taylorii*)	Rubiaceae
Ximenia caffra	Olacaceae
Zizyphus mauritana var. *jujuba*	Rhamnaceae
Zizyphus mucronata	Rhamnaceae

common names are probably remnants of a wider distribution, because they are also found occasionally in other parts of the region. These names probably date from a time before the communities in the two areas became differentiated from each other and took on the other names used for these species in the two areas. The people from whom the data were collected speak languages of the Bantu language family. The divergence of these languages and hence their

TABLE 2. Shared medicinal applications of seven species of the original 38.

Species	Application
Albizia versicolor	cough
Crossopteryx febrifuga	abortifacient
Ozoroa reticulata	stomach disorders
Piliostigma thonningii	stomach disorders
Pseudolachnostylis maprouneifolia	stomach disorders
Sesamum angolense	clearing body passages, as in smallpox and colds
Trichilia emetica	emetic

speakers from each other is estimated conservatively to have begun occurring about 2,000 years ago in the general vicinity in which these languages are now spoken (Ehret, 1973). Archaeological evidence supports this development by indicating that about 2,000 years ago there was a rapid and widespread dispersion in the southern savanna of common material culture that probably belonged to people ancestral to the present inhabitants (Phillipson, 1977). There is no evidence of historical contact between the peoples of eastern Zambia and south-central Tanzania beyond the ancestral community to which they belonged 2,000 years ago. Therefore, at least for the three or four (if *Sesamum* is included) plants with similar medicinal applications and names, we can assume a time depth for this shared use of at least 2,000 years.

Another 10 of the 38 species listed in Table 1 also have cognate names. But with the exception of two of them, which are discussed below, there are no apparent common applications; that is to say, there is no report of there being similar conditions treated by those species in eastern Zambia and south-central Tanzania. For this reason those species are not discussed here.

Four of the 38 species have strictly economic uses in common in the two areas, and one of the medicinally used species is also used economically (Table 4). Of these five, *Annona* and *Sesamum* also have similar names. The name for *Sesamum* is a shared meaning, as noted in Table 3. *Annona* is called by names that share a common prefix: *mgo-*/*mdo-* in south-central Tanzania; *mpo-* among the Ngoni and Chewa in eastern Zambia. Of course, mere prefixes do not make for cognation. Nevertheless, distribution of uses

TABLE 3. Shared names in Tanzania (T) and Zambia (Z) for medicinal plants.

Species	Name
Ozoroa reticulata	*mtukumphako*—Chewa (Z) *ntunkwangbako*—Ngindo (T)
Piliostigma thonningii	*msegesi*—Mbunga, Pogolo (T) *msekese*—Chewa, Nsenga, Ngoni, Tumbuka (Z)
Pseudolachnostylis maprouneifolia	*msolo*—unanimous (T) *msolo*—unanimous (Z)
Sesamum angolense (cognate meaning = "slippery")	*lukongela*—general (T) *delele*—Ngoni (Z)

alone suggests a great time depth for shared knowledge of these species.

The value of these cultural data is augmented by evidence drawn from the literature on pharmacological and nutritional analyses of these or related species. What follows does not represent an exhaustive search of this literature, but only a limited amount of biodynamic information appears to be available on these species, and some species have been more extensively studied than others.

The therapeutic value of a plant is determined in part by the active principle(s) it contains. Principles are compounds that form in a plant which, when used in medicinals, act upon the body's structure or functions (Githens, 1949). Among the better known principles are the alkaloids, whose best known representatives are quinine, opium, cocaine, and strychnine. There are thousands of alkaloids already known and many thousands more believed to be awaiting discovery (Schery, 1972; Schultes, 1972). Other principles that will be mentioned in this study include tannin, best known for its use in tanning hides; glucosides such as saponin, which causes foaming when added to water and so is common in toothpastes and soaps; cardiac and anthelmintic glucosides that affect heartbeat and circulation or expel worms; and resins, oils, and occasional other principles that are not classed in any of the above. New principles are constantly being discovered. So, too, are there still thousands of plant species of which we know very little or nothing at all (Kreig, 1964; Schultes, 1972).

Traditional doctors are not known to use terms like those above to explain why they use a specific plant for a specific condition. Nevertheless, the applications generally indicate the kind of pharmacological actions that can be expected (Hänsel, 1972). Through selection, traditional doctors have also taken their medicines through "clinical trials" (Malone, 1983). The 11 species cited in this study appear by other evidence to be of long-standing use in east-central Africa. We may therefore anticipate some confirmation of their utility from evidence on their compounds that results from biochemical screening of these or related species.

The species *Albizia versicolor*, whose shared application is for cough, has received no research itself. However, studies of the genus *Albizia* indicate it contains a saponin called *musennin* (Steinmetz, 1961; Watt & Breyer-Brandtwijk, 1962). Githens (1949) suggests that saponins have an expectorant quality, for they cause increased secretion in respiratory passages and loosen mucus. It may be for this action that the species is used as a remedy for cough.

Crossopteryx febrifuga derives its name from an early association of the species with antifever activity (Githens, 1949). Other findings dispute its value for fever (Watt & Brayer-Brandwijk, 1962). Moreover, it is not reported to be applied for that condition either in eastern Zambia or in south-central Tanzania. In those areas the species is used medicinally as an abortifacient. Research shows that it contains alkaloids, though there is

TABLE 4. Shared economic use of five species of the original 38 selected for the study.

Species	Use
Annona chrysophylla	fruits eaten
Diospyros kirkii	fruits eaten
Sesamum angolense	leaf vegetable
Swartzia madagascariensis	fish poison
Uapaca kirkiana	fruits eaten

some dispute over the specific alkaloids involved (Oliver-Bever, 1983) and they are all being called by one name, *crossopternine* (Watt & Breyer-Brandwijk, 1962). Alkaloids, by their nature, are able to promote menstrual discharge (Githens, 1949). Thus *Crossopteryx* would appear to be tentatively confirmed at least in its role as an abortifacient.

Ozoroa reticulata has been little investigated. Studies indicate that its bark contains tannin (Watt & Breyer-Brandwijk, 1962) of which there are different kinds, some soluble and others not. The latter kind seems likely for *Ozoroa,* for relatively insoluable tannins are best for internally used medicines in the treatment of diarrhea, dysentery, and relief of stomach inflammation (Githens, 1949). These may be the kinds of stomach disorders that *Ozoroa* is used to treat in the region, though these disorders have only been generalized in this study and nothing specific is known about them. Volatile oils have also been found in association with the tannin, at least in other species of *Ozoroa.* They, too, are active in treatment of stomach disorders (Githens, 1949). Recently an active principle, Moronic Acid 1, has been extracted from the root bark of a related species in Tanzania, *O. mucronata,* and this principle is said to have antimicrobial activity (Horstettmann-Kaldas & Nakanish, 1979) that might include stomach parasites.

Less information is available on *Piliostigma thonningii* and *Pseudolachnostylis maprouneifolia. Piliostigma,* at least, is said to yield tannin (Watt & Breyer-Brandwijk, 1962), a principle already noted above for its role in treatment of stomach disorders. No research has emerged on *Pseudolachnostylis maprouneifolia* other than a Tanganyika government chemical report of 1956 reporting a lack of toxicity in the species (Watt & Breyer-Brandwijk, 1962), although toxicity is a characteristic of the Euphorbiaceae, of which it is a member. It may be this evidence that led Githens (1949) to consider its use as a purgative to be of doubtful value. However, several species in the Euphorbiaceae family are said to make excellent purgatives, for they contain antidiarrheal agents and anthelemintics (Lewis et al., 1977). *Pseudolachnostylis* is probably the least significant species on this list, medicinally speaking, and would not seem to warrant further research. It is one of seven species of a genus restricted to south tropical Africa (Palmer & Pitman, 1972).

Sesamum angolense seems, by the evidence, to be appropriately used in east-central Africa. Cooked leaves are placed in body orifices to keep them from closing due to smallpox pustules. An infusion is used for colds (perhaps as an expectorant?). The mucilaginous principle that characterizes the leaves of *Sesamum* has a cathartic value (Githens, 1949) for which the reported applications for the species seem to suggest it is used.

The final medicinal species, *Trichilia emetica,* is considered an emetic, as its name suggests. The Meliaceae, to which it belongs, is characterized in part by its several emetic-acting species. This family is identified with tannin and resin (Watt & Breyer-Brandwijk, 1962) and both principles are important in emetic medicines (Githens, 1949).

Of the economic plants with which I am concerned, three are used as foods and one for fish poison. One species, *Annona chrysophylla,* which belongs to an important tropical fruit family (Nicholson et al., 1969), produces edible fruit. Species of Annonaceae produce fruit known popularly as "custard apples," "sweet" and "sour sop," etc. The fruits are high in niacin and sugar (Fleuret, 1979), and vitamins B and C (Watt & Breyer-Brandwijk, 1962).

Diospyros kirkii belongs to the ebony family, Ebenaceae, and its fruits are eaten in eastern and southern Africa, as are those of a related species, *D. mespiliformis* (Waite, 1981; Watt & Breyer-Brandwijk, 1962). No analysis has been made of their fruits; indeed, Watt and Breyer-Brandwijk (1962) marvelled that *D. mespiliformis,* the only species for which they had data, was used for food, for the plant contains quantities of tannin. They noted that *D. mespiliformis* is used as a famine food. Studies on related *Diospyros* species in West Africa show they contain vitamin K (Kerharo & Adam, 1974).

Uapaca kirkiana, the third fruit plant in this survey, is also a fruit that is important during famine. Its pulp has been found to contain some ascorbic acid (Watt & Breyer-Brandwijk, 1962).

Fleuret (1979) has pointed out that sources on food plants agree that wild fruits are mainly eaten by children as snack food. However, under certain conditions, such as famine, these fruits become adult food as well.

Dealing with *Sesamum angolense* again, *Sesamum* is known to be an ancient source of oil in Africa and other parts of the world where it

has been introduced. It is not used that way in east-central Africa, where its only food use is as a relish prepared from the mucilaginous leaves. Information from the West African *Sesamum* species, *S. indicum,* indicates that there are tannins and other acids in the leaf which may make it useful as a mild laxative (Githens, 1949), a function it might have as a food. No studies have been done on the leaves, but leaf vegetables are known to be important sources of proteins, calcium and other minerals, vitamin A, and niacin (Fleuret, 1979).

Finally, there is the fish poison plant, *Swartzia madagascariensis* (Fabaceae, subfamily Papilionoideae). The fruit of this species has yielded a saponin that is highly toxic to fish, but in the dosages used to kill fish it is not toxic to mammals (Watt & Breyer-Brandwijk, 1962). It takes from 75 minutes to 12 hours to kill the fish, depending on the dosage used. The potential economic value of this species has not been explored, though it could possibly also be investigated for insecticide uses, as many fish poisons have this application as well (Lamba, 1970).

The literature on the biodynamic components of the species studied here provides considerable support for the applications and other uses. Without exception, each use is borne out by biochemical analysis undertaken for these species or members of the same genus. Githens (1949), who pioneered comparative studies of African medicinal plants, suggested that in the absence of chemical studies, usefulness of species can be assumed if similar use is found over a wide geographical area. This study goes beyond that. Not only have similar uses for these species been mapped here, but they were also compared with the phytochemical and medicinal literature from which evidence has been drawn that lends support to the particular applications for the species.

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SOME DISTRIBUTION PATTERNS IN THE LICHEN FLORA OF SOUTH AFRICA

OVE ALMBORN[1]

ABSTRACT

A diversity of distribution patterns exhibited by South African lichens is presented, including some ubiquitous (more or less cosmopolitan) species and a number of endemics. These are few compared with the high number of endemics among the vascular plant flora. Steppe and desert species best represented in the arid areas, montane species growing at high altitudes, oceanic species predominant in humid wooded districts in the south and the east, and maritime species (mainly confined to sea rocks) form fairly well-defined groups. Species also known from other regions in the Southern Hemisphere (South America and/or Australia/New Zealand) are highly interesting to the phytogeographer. A fascicle *Lichenes* for *Flora of Southern Africa*, with the collaboration of many specialists in lichen taxonomy, is being planned.

RÉSUMÉ

L'auteur présente une diversité de types de répartition pour les lichens d'Afrique du Sud, y compris des espèces omniprésentes (plus ou moins cosmopolites) et un nombre d'espèces endémiques. Celles-ci sont peu nombreuses si on les compare au nombre élevé d'espèces endémiques parmi la flore des plantes vasculaires. Les espèces des steppes et du désert qui sont le mieux représentées dans les régions arides, les espèces montagneuses des altitudes élevées, les espèces océaniques qui prédominent dans des districts forestiers humides du sud et de l'est, et les espèces maritimes (qui se trouvent surtout sur les rochers marins) forment des groupes assez bien définis. Des espèces connues d'autres régions de l'Hemisphère Sud (Amérique du Sud et/ou Australie/Nouvelle Zélande) sont très intéressantes pour la phytogéographie. Une section *Lichenes* pour la *Flore de l'Afrique Australe* est projetée avec la collaboration de nombreux spécialistes de la taxonomie des lichens.

HISTORICAL SKETCH

The first lichen recorded from South Africa was *Lichen chrysophthalmus* L., mentioned by Linnaeus in *Mantissa Altera* (1771), one of the last works he published. The material came from the Danish botanist J. G. Koenig, who travelled widely with the Danish East Asiatic Company. It is now known as *Teloschistes chrysophthalmus* (L.) Th. Fries and is widely distributed mainly in tropical and subtropical areas all over the world. In South Africa it is a fairly common lichen everywhere on trees and shrubs.

The next contribution came 10 years later (1781) when Linnaeus filius (*Supplementum Plantarum*) described four species of lichens collected by Carl Peter Thunberg, the "father of South African botany," who spent three years (1772–1775) at the Cape. These four species are well known today (under other names) as belonging to the endemic element, known to occur only in South Africa. They are: *Lichen capensis* [now *Teloschistes capensis* (L. f.) Vain.]; *L. flammeus* [*Xanthoria flammea* (L. f.) Hillm.]; *L. verrucosus* [*Siphula verrucigera* (J. F. Gmel.) R. Sant.]; and *L. viridis* [*Dermatiscum thunbergii* (Ach.) Nyl.].

Thunberg published several works on the Cape flora covering the whole plant system. In his final *Flora Capensis* (1823) he listed a total of 39 lichen species. Most of these were described by Erik Acharius, a Swedish physician considered as the founder of lichenology as a special branch of plant systematics. His herbarium is at Helsinki, but the whole Thunberg collection of lichens at Uppsala was seen by Acharius and, in most cases, contains the best material for selecting lectotypes.

The 19th century saw numerous lichens collected in South Africa, mostly by botanists principally interested in vascular plants, and described by various specialists in Europe. The famous German collectors Drège, Ecklon, and Zeyher gathered several hundred thousand specimens in the 1820s–1830s (among them a number of lichens), which they sold to various herbaria. Protection of nature was not known at that time! Collectors from the later part of the 19th century included the Austrian Heinrich Wawra, originally a surgeon in the navy who travelled

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widely, was later elevated as "Ritter von Fernsee," and who collected lichens at the Cape. These were described in 1861 by the Italian Massalongo in Verona, who recorded 48 species. The types are in Verona. Another contribution came from a British expedition sent in 1875 to observe the transit of the planet Venus. They collected lichens at the Cape mainly on Table Mountain. These were enumerated by the English clergyman Crombie, who recognized 96 species; 34 of these were described as new by the Finnish lichenologist William Nylander. This type material is in the British Museum and in Helsinki. In the early 1890s, the German physician Stizenberger published a major work called *Lichenaea Africana,* in which he described a great number of new species, many of them from South Africa. Some of his contributors were Peter MacOwan, a well-known botanist, later director of the Botanical Garden in Cape Town; Wilms, a German apothecary, for many years living at Lydenburg in the Transvaal; and Anton Rehmann, a Polish botanist who travelled widely in South Africa in the 1880s. All material seen by Stizenberger is at the Technical University at Zürich (ZT).

These scattered notes may illustrate an important fact for further work on a South African lichen flora. Almost all types of new species described from South Africa are in various European herbaria. Some of them lend material, some are not well curated, and a personal visit is often necessary in order to find the needed specimens. This situation is, of course, well known also to those working on other groups of plants.

During the first part of the present century some efforts were made to survey the many lichens described in the literature and stored in herbaria. P. A. van der Byl, professor at Stellenbosch and mainly interested in fungi and phytopathology, collected lichens in the 1920s and 1930s, which he sent to various lichenologists for determination, mainly Zahlbruckner in Vienna and Vainio in Turku (Finland). His lichen herbarium is kept separately at the University of Stellenbosch and is an important source of our knowledge of South African lichens. In 1935 he started a series of surveys of some lichen groups in all 73 species. He included keys, short descriptions, records of distribution and ecology, and provided photographs of the species. However, his descriptions were founded on limited material compiled from various authors; no critical revision of the species, including studies of type material, was involved.

In 1950, Dr. Ethel M. Doidge in Pretoria published the important *South African Fungi and Lichens* (Doidge, 1950). The lichens formed a special part (ca. 150 pages) and followed Zahlbruckner's system, which was predominant in lichen taxonomy in the first half of this century. Her list of lichens includes fairly completely all species and other taxa reported from southern Africa, including the areas then known as Basutoland, Swaziland, Bechuanaland, Southwest Africa, Rhodesia, and the southern parts of Zambia, Malawi, Mozambique, and Angola. The records were taken from the literature and, to a lesser extent, from unpublished determinations of material in herbaria in South Africa (Cape Town, Pretoria, Stellenbosch) and England (British Museum, Kew). All known localities were recorded for each species, and detailed literature references were given. There are, however, no descriptions and no taxonomic revision of the material. Nevertheless, it is an indispensable account of what was known about the lichen flora of southern Africa up to 1945.

Doidge recorded 1,159 species (and a number of varieties and forms) from the area as delimited by her. This number of species is fairly high if we consider that many parts of southern Africa have little or no tree vegetation and thus lack most of the epiphytic lichens. For comparison may be given some totals from other groups of cryptogams: Ascomycetes 835 spp., Basidiomycetes 1,704 spp. [Doidge (1950) and referring to the area in her delimitation], Musci ca. 600 spp. (Magill & Schelpe, 1979), Hepaticae 298 spp. (among them 153 endemes) (Arnell, 1963), Pteridophyta ca. 300 spp. (Schelpe, pers. comm.). However, compared to the number of phanerogamic plants in the Republic only (ca. 20,000 spp.), the number of lichen species is remarkably low.

One might believe that the compilation of a lichen flora of southern Africa would be an easy task if we use the rich material presented by Doidge and provide her species with descriptions and keys. Such a procedure would soon meet with a lot of problems. Many of the determinations quoted by her were made by different persons and at different times. The same specific epithet therefore may refer to different species. The need for thorough taxonomic revision of many groups is urgent. There are still very few modern world monographs of lichen genera. There are also too many so-called "endemic species" described mainly by Zahlbruckner and

Vainio, often based on poor specimens and known from the type locality only. It is well known that these two famous lichenologists seldom read papers other than their own, at least at the end of their active period. As we all know, the simplest way of solving a taxonomic problem is to describe a new species.

It is still premature to express any definitive statement about the number of lichen genera and species in South Africa. Two hundred (perhaps 300) species listed by Doidge are most probably synonymous. On the other hand, there is good evidence that at least twice as many "good" species will be added to the sum. I would like to venture a guess: the end of this century will reckon with 1,500–1,800 species of lichens.

One important question arises: what is a "good" lichen species? The species concept in lichenology is far from clear. Conservative taxonomists want a combination of several stable characters to be convinced of the validity of a species. Some chemotaxonomists consider the presence or absence of a certain chemical substance (or sometimes several substances) to be sufficient for distinguishing a species even if there is no visible morphological difference. An intermediate school argues that a combination of chemistry and geographical distribution forms an ideal species.

Phytogeographical Sketch

The great majority of lichen species recorded from South Africa is still imperfectly known as to taxonomy and distribution and cannot be included in any phytogeographical pattern. I have made an effort, however, to distinguish some distributional groups. They have been selected according to somewhat different principles and are therefore partly overlapping. I have chosen a small number of species representative of each group.

1. *Ubiquitous species with a more or less worldwide distribution.* These are well represented in South Africa without any distinct phytogeographical pattern.

Buellia punctata, Candelaria concolor, Lobaria pulmonaria, Peltigera canina, Physcia stellaris, Xanthoria parietina.

A number of lichens common in the Northern Hemisphere are absent in South Africa, for example, the reindeer lichen, *Cladonia rangiferina* (a related species present at high elevations, e.g., Table Mountain), *Parmelia sulcata,* and the genera *Cetraria* and *Evernia.*

2. *Steppe and desert species.* A considerable number of saxicolous and terricolous species have their distribution concentered in the arid areas of Namibia, Namaqualand, Kalahari, and Karoo.

Acarospora fuscata, Acarospora schleicheri, Diploschistes actinostomus, Heppia euploca, Psora decipiens, Xanthoparmelia spp.

Many of them are characteristic of arid districts in other parts of the world.

3. *Montane species.* As a rule saxicolous or terricolous, they are usually found at high altitudes only, typically above 1,000 m.

Dermatiscum thunbergii, Lasallia capensis, Lasallia papulosa, Neofuscelia (several spp.), *Pertusaria leonina, Placopsis gelida, Rhizocarpon geographicum, Solorina simensis, Stereocaulon* spp., *Usnea pulvinata, Xanthoria elegans.*

4. *Oceanic species.* These are predominant in the fairly humid, wooded areas of the south and east, e.g., the slopes of Table Mountain, Knysna and Grahamstown districts, the south and east slopes of the Drakensberg Mountains, and the Transvaal Mountains. The annual rainfall amounts to ca. 800–2,000 mm spread over most of the year. A considerable number of species belong here, many of them with a worldwide distribution in oceanic areas.

Heterodermia leucomela, Normandina pulchella, Pannaria rubiginosa, Parmelia austrosinensis, Parmelia crinita, Parmelia reticulata, Pseudocyphellaria aurata, Pseudocyphellaria crocata, Sticta fuliginosa, Teloschistes flavicans, Usnea rubiginea.

5. *Tropic-oceanic species.* These are mainly restricted to northern Natal (Zululand), eastern Transvaal, and Mozambique, where the mean annual temperature is high, the winters mild, and annual precipitation high.

Glyphis cicatricosa, Graphina acharii, Gyrostomum scyphuliferum, Parmelia andina, Parmelia dilatata, Strigula elegans, and other foliicolous lichens.

6. *Maritime species.* Restricted to maritime rocks, they constitute an ecological group not directly comparable to the previous.

Caloplaca sublobulata, Combea mollusca, Roccella arnoldii, Roccella hypomecha, Roccellina capensis, Xanthoria capensis.

7. *Endemic species of South Africa.* Represented within groups 2–6, they afford a number

of interesting problems. Among the lichens recorded by Doidge in 1950 there are four genera (all monotypic) and some 300 species considered endemic in southern Africa. Among the genera, only *Combea*, included with the maritime species, is a unique (perhaps even spectacular) genus. The other three need further investigation. Another new genus, *Eremastrella*, was described in 1955 from the Drakensberg by the German botanist Stephan Vogel. It is now regarded as identical with a lichen described from Australia in the 1840s, *Lecidea crystallifera*, and known as *Eremastrella crystallifera*. This pattern of distribution (south-hemispheric and bicontinental) has proven to have many counterparts.

As stated earlier, many so-called endemes, especially among the crustose lichens, are described briefly and vaguely and on scanty material. Many of them will be reduced to synonymy when richer material is available.

However, there are a number of true endemes in the South African lichen flora. Several of them are among the lichens found by Thunberg 200 years ago. Some examples include:

Neofuscelia cafferensis, Neofuscelia caliginosa, Siphula verrucigera, Teloschistes capensis, Toninia bumamma, Xanthomaculina hottentottum, Xanthoria flammea.

The number of true endemes will most probably prove to be considerably higher in the future; but nevertheless, as in other groups of cryptogams, there will be few equivalents to the high numbers of endemic families, genera, and species known from the phanerogamic flora.

It is also becoming more evident that South Africa has many lichen species in common with central Africa, which is not surprising, but also with South America, the southern parts of Asia, Australia, and New Zealand. Examples of this south-hemispheric element are: *Caloplaca subnitida, Cladonia polia, Cornicularia epiphorella, Neofuscelia imitatrix, Neofuscelia squamans, Neofuscelia verisidiosa, Neofuscelia verrucella, Parmelia andina.*

These connections between the continents in the Southern Hemisphere are difficult to explain. Long-distance dispersal during recent times seems unlikely. Instead, I am convinced that these patterns of distribution must be referred to conditions prevailing on our planet in early geological periods.

Wagener's theory of Continental Drift (from the 1920s) of the former connection (the Gondwana continent) and the later separation of the continents in the Southern Hemisphere, which was first met with considerable scepticism but now generally accepted, may solve many problems of lichen distribution patterns.

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MICROCOMPUTER-AIDED DESCRIPTION AND COMPARISON FOR BRYOPHYTES—A PROTOTYPE

ALAIN EMPAIN[1]

ABSTRACT

The powerful computer language FORTH (standard for the astronomical community) is used to develop a high-level language adapted to taxonomical needs. Leaf shapes of mosses are used to demonstrate hierarchical code for descriptor names, comparison between taxons, and synthesis (as text or as high-resolution graphics).

RÉSUMÉ

Le langage informatique FORTH (utilisé comme norme en astronomie) est employé ici afin de développer un langage de haut niveau pour des besoins taxonomiques. Les formes des feuilles de mousse sont utilisées pour démontrer le code hiérarchique des descripteurs, les comparaisons entre taxons et la synthèse textuelle ou graphique.

Numerical taxonomy began in the late 1950s (for an extended bibliography see Sneath & Sokal, 1973), aided by the newly treated computers for repetitive calculations needed by statistics. These computers were used in a batch environment, where data are gathered on paper, then punched on cards and submitted to the computer, all without access to the program flow.

Omnipresent cheap microcomputers have sharply changed this procedure; interactive applications are now presented for bryophytes at the personal level (Magill, 1982; Frahm, 1983; Empain, 1985a, 1985b, 1987). The aim for our work is to provide a general tool, like a desk calculator with an extensive and powerful keypad. This tool proves to be really more flexible than a collection of one-purpose programs.

The exceptional computer language FORTH applies well to such a goal. Due to its strange appearance, a short introduction to this language is needed, before coming to taxonomical developments (Brodie, 1981).

WHAT IS FORTH?

FORTH is an unusual language, joining many rather antithetical advantages without their usual drawbacks. Unlike many other languages (starting from a theoretical definition and tending to the best possible implementation), FORTH was developed by Moore (early 1970s) within a practical context. It was intended to give most of the advantages of ASSEMBLER with all the possibilities of a structured high-level language like PASCAL.

It is now the international standard for the astronomical community and it receives a growing interest for serious applications ranging from robotic and data base management to medical care.

a. FORTH uses a data stack and the Reverse Polish Notation (RPN, such as Hewlett-Packard for their calculators) for speed, efficiency, and total suppression of parentheses. Example:

Basic	((5 + 4) • 7) + 2	(11 items)
FORTH	5 4 + 7 • 2 +	(7 items)

b. Each new procedure ("WORD") is compiled for speed but can be used as a *direct command* like an interpreted BASIC instruction.

c. The philosophy of FORTH favors top-down programming and very short definitions; even the most complex situation can be broken down easily into small logical pieces and *fully tested* (this is not a trivial task in many other languages). A small example:

We need to prompt for cell dimensions and to display the ratio. The top WORD is intuitively defined (the colon opens the definition of LENGTH/WIDTH and the semicolon closes it).

```
: LENGTH/WIDTH   ASK-LENGTH
  ASK-WIDTH   COMPUTE-RATIO
  PRINT-RATIO ;
```

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TABLE 1. Description of some levels of the hierarchical code for character names.

Level 1	Level 2	Level 3	Level 4
0 Generalities			
1 Whole plant	1 on stem	1 outline	1 length
2 Leaf →	2 on branch →	2 longit. vol.	2 width
3 Paraphylls	3 on sec. branch	3 transv. vol.	3 ratio
4 Sexual organs	4 perigonial	4 cells	4 wall thickness
5 Sporophyte	5 perichaetial	5 standard cells →	5 wall color
6 Vegetative prop.	6 innovations	6 base	.
7 Protonema	.	7 border	. (reserved)
8 Rhizoids	. (reserved)	8 nerve	.
9 Stem	.	9 cross-section	
.		.	
. (reserved)		. (reserved)	
.		.	

Each step can now be defined with lower WORDS such as CR for carriage return . . .

```
: ASK-LENGTH      CR  ." LENGTH ?"
                      INPUT ;
: ASK-WIDTH       CR  ." WIDTH ?"
                      INPUT ;
: COMPUTE-RATIO       /
                  ; (division operator)
: PRINT-RATIO  CR  ." RATIO = " . ;
```

Now, when we type LENGTH/WIDTH, we are prompted for length and width data and the ratio is typed; we can also insert this WORD within a higher level WORD.

```
: CALC-ON-CELL    WALL . . . . . .
                      LENGTH/WIDTH;
```

d. FORTH is an ever growing dictionary of WORDS, without any difference between the original kernel of WORDS and the newly added WORDS. Moreover, an original WORD can be redefined to obtain a modified behavior or synonyms. Example:

- for short

```
  : L/W  LENGTH/WIDTH;
                  (L/W is now a synonym)
```

- for translation in french

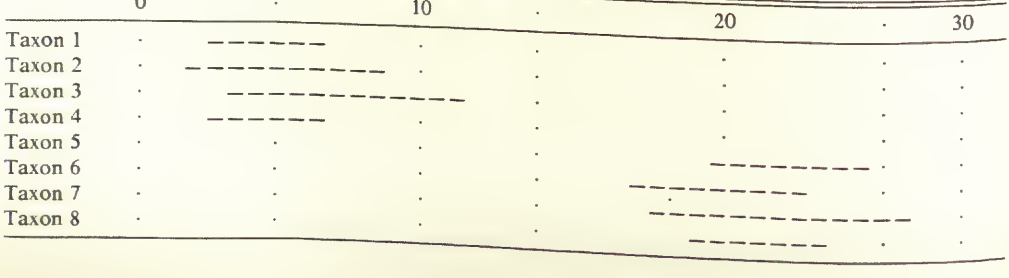
```
  : LONGUEUR/LARGEUR
                  LENGTH/WIDTH;
```

- for security

```
  : COMPUTE-RATIO     DUP 0 =
    IF ( =0)     CR ." I CANNOT DIVIDE
                          BY 0 ! " QUIT
    ELSE (<>0)   CR ." OK FOR DIVIDE
                          CHECK"
    THEN  /  ;
```

e. New language features can easily be implemented (unlike most other languages): new struc-

TABLE 2. Example of the graphical display of a taxonomic variable (here compressed within 32 classes). The homogeneity of the two sets of taxa (1–4, 5–8) can be seen visually and simply.



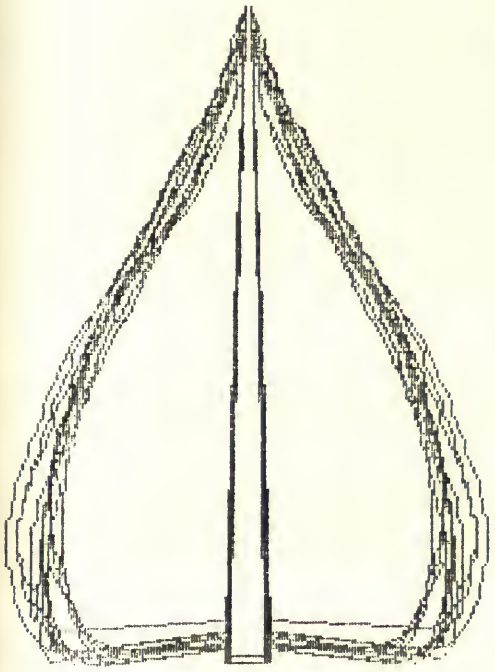


FIGURE 1. Mean outline of the leaf is obtained by superimposing 16 specimens (*Brachymenium acuminatum*, copper mines of Zaire). Thirteen simple characters are used to encode leaf outline. Smoothing is due to splines interpolation (extracted from Empain, 1987).

tures (CASE as in PASCAL . . .); new data types or WORDS classes (see taxonomical variables). In fact, FORTH is a *tool-language* that allows definition of specially designed higher level *language*, where simplicity and easy use are the main goal. For an End-User Taxonomist, the following sentences are meaningful, easy to use, and potentially powerful:

```
SPECIES-1  is  BRACHYMENIUM
                 PHILONOTULA (load it)

SPECIES-2  is  BRACHYMENIUM
                 ACUMINATUM (load it)

COMPARE
   or
SPECIES-1  is  DIALYTRICHIA
                 MUCRONATA

LEAF   DRAW   HARD-COPY
```

TABLE 3. Example of automatic sentences production. Type LEAF-DESCR to generate the following text (for the current taxon). References for shapes are taken from Magill, 1981.

Specimen Name: *Splachnobryum obtusum*	
Most Similar Shape	Number of Discrepancies
obovate	0
spathulate	1
oblong	2
lingulate	3

Leaf not curved, not asymmetrical, without auricles; apex rounded.
Nerve simple, reaching ½ to ¾ of the leaf.

APPLICATION TO BRYOLOGY

CODIFICATION FOR CHARACTER NAME

A hierarchical code (4 levels) provides many advantages for the user and programmer. The two left digits point to the entity involved (stem leaf, capsule, etc.) and the two right digits specify the evaluated parameter (Table 1). Example:

"2451" means
2: leaf
4: perigonial
5: standard cells (at ⅔ of the lamina)
1: length
and can be decoded as "Perigonial leaf, length of standard cells."

"2151" means "Stem leaf, length of standard cells," etc. Some technical properties are useful for our application:

- With some practice, at least the higher levels are easily remembered.
- Full text decoding is easily implemented for automatic generation of paragraphs.
- The code based on hexadecimal notation (each digit can take 16 values) has the same format as an integer number in FORTH and can be worked very easily with all the arithmetic and logic operators.
- For comparison between heterogeneous sets of characters, a WORD can be implemented for automatic reorganization, using lists of character codes embedded within the files.
- It is even possible to encode freely some descriptions gathered in the literature, using the descriptor code as a prefix for the value encoded and relying on a reorganizing WORD.

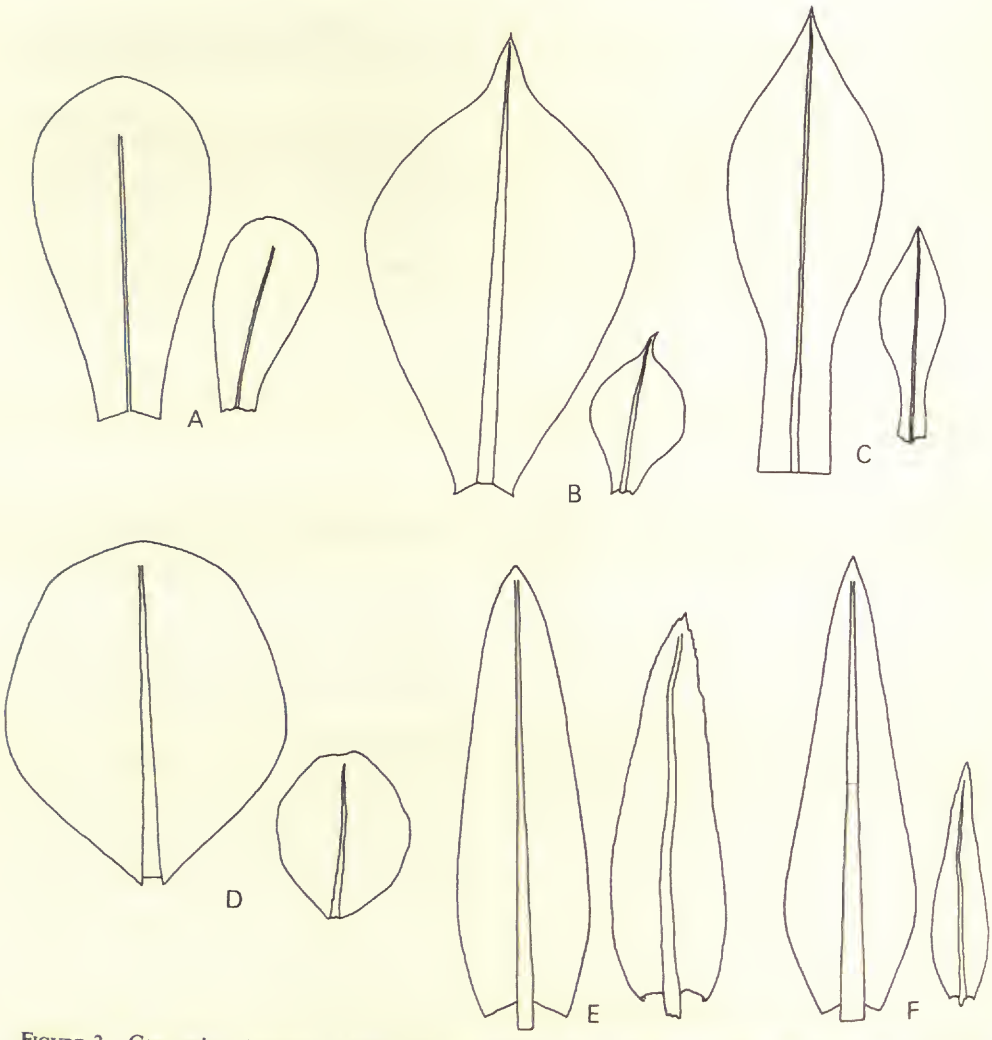


FIGURE 2. Comparison between original shapes (smallest picture) and encoded shapes redrawn in high-resolution with the simple WORDS: LEAF (for leaf set up); SMOOTH (for splines calculation); DRAW (for high-resolution display); HARD-COPY (for printer output).—A. *Splachnobryum obtusum.*—B. *Splachnum sphaericum.*—C. *Physcomitrium collenchymatum.*—D. *Mnium pseudopunctatum.*—E. *Aulacomnium androgynum.*—F. *Pohlia cruda.* (Extracted from Empain, 1987.)

SYNTHETIC DESCRIPTION OF A TAXON

Given a list of encoded specimens, or a list of higher-level taxa, a standardized description of a synthetic taxon can be computed.

For each character, statistics such as the minimum, the maximum, the percentiles, the median, etc., are computed and taken into account for the next stage.

A *taxonomic variable* is defined by two components, the two allowable value limits for a given character of a given taxon [based on confidence interval, observed range, or observed percentiles (5–95%)]. Depending on the type of character, the highly heterogeneous values (classes, numbers, dimensions, etc.) can be standardized within a fixed number of classes. For example, a taxonomic variable of 32 classes can be compressed within the space of one byte (space needed for one character storage) for routine comparisons, allowing speed and space-saving

TABLE 4. Comparison between two taxa: display of the most significant differences (disjunction of ranges begins at the value 8).

Comparison between: *Cinclidotus nigricans* / *Dialytrichia mucronata*	
Discrepancies for:	Difference Coefficient:
2116	3
211B	16
Decoding ?	
2116 decodes as "STEM leaf, width at ¾ of the length"	
211B decodes as "STEM leaf, length of pulled nerve"	

TABLE 5. Selection of the nearest taxa, according to a rejection level of cumulative difference.

Sample: Empain 1611	
Nearest Taxa	Cum. Diff.
→ *Cinclidotus aquaticus*	0
Cinclidotus danubicus	3
Cinclidotus fontinaloides	7

for disk files. These manipulations (classification + compression) degrade the original values by only a small percentage.

Aside from speed and space, standardization of variables opens the door to unified operations such as nonparametric tests and standard graphic displays (Table 2).

For the leaf, the individual values can be superimposed to give a graphically mean picture (Fig. 1).

DECODING THE DATA

The data can be restored to text by simple procedures:

- decode the descriptor name;
- decompress the data;
- print the interval values or decode the class definitions, e.g., 4 → "slightly less thick";

or the data can be drawn, as for the leaf (Fig. 2), with some additional text (Table 3).

COMPARISON BETWEEN TWO TAXA

For each character, a coefficient of difference is computed. It takes into account the allowable range of the two taxonomic variables. "Good" characters are automatically more discriminant than "bad" variable characters. The choice of an acceptable level for displayable differences allows one to select a fairly large amount of characters on the screen (Table 4).

SELECTION OF THE NEAREST TAXA WITHIN A SET

The nearest taxa to a sample can be displayed according to a rejection level for a cumulative difference (Table 5). The extended comparison (see previous paragraph) with the most interesting taxa allows one to identify eventual discrepancies and to discard or to accept the determination (a personal decision).

DISCUSSION

Many decisions must yet be made about descriptors, scales, and which statistical tests to use.

A standard minimum subset of descriptors must be defined: it can be very useful for basic exchange and in particular for type descriptions. For the monograph, a more exhaustive set can be created, thanks to the reserved values at each level of the code: some special characters can be described and studied with the same FORTH WORDS.

Many WORDS are now implemented, as well as others not detailed here (statistical tests, Fast Fourier Transform analysis, semiautomated measurements at the microscope, etc.), creating some integrated tools for the bryologist. Other WORDS are being tested and are not yet integrated (machine-independent file support).

Decisions about compression of data need attention. Perhaps the best solution is the choice of a double set of data, one set intended for precise description (data not compressed) and the other intended for fast selection routine (data compressed within 16 or 32 classes).

FORTH permits easy changes between alternate procedures (by vectoring); tests using different definitions for allowable limits or for difference coefficients must be performed to settle down a routine procedure.

Furthermore, at a practical level, FORTH is implemented on virtually all computers (micro to mainframes) and is well defined by an international standard; transporting software between very different machines is not difficult, even for the machine-dependent disk operating system.

CONCLUSION

This prototype for an integrated set of FORTH WORDS is intended to raise discussion and crit-

icism. For a limited and individual purpose, the implemented kernel is rather operational, needing mainly some more integration between the pieces (file use, statistics, etc.).

The potential power of "taxonomic" FORTH lies in the perspective of data exchange and standard type descriptions. For this more distant goal, a refined and widely accepted code must be developed, in the spirit of the future *Illustrated Guide to Bryological Terms* (for a first-stage publication see Magill, 1981).

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MORPHOLOGY AND BIOGEOGRAPHY OF SAXICOLOUS *CALOPLACA* IN SOUTHERN AFRICA

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ABSTRACT

Caloplaca is one of the largest lichen genera, the total number of species estimated at 500. Doidge (1950) included over 40 saxicolous *Caloplaca* from southern Africa. Her list, however, was compiled from literature, and a considerable reduction of species is expected in the planned new Lichen Flora of Southern Africa. The morphological variation of nine saxicolous species locally common in southern Africa are described and illustrated. The species belong to several different morphological types, e.g., crustose thallus, cracked-areolate thallus, areolate thallus with marginal lobes, thallus formed of smaller or larger lobes, and subfruticose thallus. All species develop apothecia, but two mainly reproduce asexually in clones with isidia. Four species are endemic to southern Africa, *C. almbornii* Kärnef., *C. bonae-spei* Almborn & Poelt, *C. elegantissima* (Nyl.) Zahlbr., and *C. haematodes* (Massal.) Zahlbr. Three species are known mainly from southern Africa but also occur in South America, *C. isidiosa* (Vain.) Zahlbr., *C. ochraceofulva* (Müll. Arg.) Jatta, and *C. subunicolor* (Nyl.) Zahlbr. *Caloplaca sublobulata* (Nyl.) Zahlbr. is known mainly from Africa and southernmost South America but, like the most widely distributed species *C. cinnabarina* (Ach.) Zahlbr., also occurs in Australia.

RÉSUMÉ

Caloplaca est l'un des genres de lichens les plus vastes et on estime qu'il existe un nombre total de 500 espèces. Doidge (1950) englobait plus de 40 espèces saxicoles de *Caloplaca* provenant du sud de l'Afrique. Mais sa liste avait été établie à partir de la littérature et on devrait constater une réduction considérable d'espèces dans la nouvelle Flore des Lichens d'Afrique Australe actuellement en projet. L'auteur décrit et illustre ici la variation morphologique de neuf espèces saxicoles communes localement en Afrique australe. Les espèces appartiennent à différents types morphologiques, soit thalle crustacé, thalle fissuré-aréolé, thalle aréolé avec des lobes marginaux, thalle de lobes plus ou moins grands, et thalle subfruticuleux. Toutes les espèces developpent des apothèces, mais deux d'entre elles se reproduisent asexuellement en clones par des isidiums. Quatre espèces sont endémiques à l'Afrique australe, *C. almbornii* Kärnef., *C. bonae-spei* Almborn & Poelt, *C. elegantissima* (Nyl.) Zahlbr. et *C. haematodes* (Massal.) Zahlbr. Trois espèces sont connues principalement en Afrique australe mais se trouvent aussi en Amérique du Sud, *C. isidiosa* (Vain.) Zahlbr., *C. ochraceofulva* (Müll. Arg.) Jatta et *C. subunicolor* (Nyl.) Zahlbr. *Caloplaca sublobulata* (Nyl.) Zahlbr. est connu principalement en Afrique et dans la partie la plus australe de l'Amérique du Sud, mais, comme pour les espèces à répartition la plus large, *C. cinnabarina* (Ach.) Zahlbr., elle se trouve aussi en Australie.

The genus *Caloplaca* Th. Fr. is one of the largest lichen genera. Santesson (1970), who investigated the chemistry of some 230 species, estimated the total number of species to be near 500. It remains the largest genus of Teloschistaceae. Many generic segregates such as *Blastenia* (Massal.) Th. Fr., *Huea* Dodge & Baker, *Gasparrinia* Tornab., and *Kuttlingeria* Trevis. have not been accepted. Haefellner & Poelt (1979) showed that the group of species with plurilocular spores, separated under the generic names *Xanthocarpia* Massal., *Meroplacis* Clements, and *Triphthalmidium* (Müll. Arg.) Gyelnik, did not form a natural group, but seemed to have evolved from at least three different species groups within *Caloplaca*. Recently, Poelt & Pelleter (1984) also demonstrated that the subfruticose species, earlier separated in *Caloplaca* section *Thamnonoma* Tuck. or in the genus *Polycauliona* Hue, were derived from different species groups within section *Gasparrinia* (Tornab.) Th. Fr. A more detailed discussion of the circumscription of genera within Teloschistaceae has been published by Almborn (1963) and by Poelt & Haefellner (1980).

In southern Africa *Caloplaca* probably comprises over 50 species. Doidge (1950) listed over 40 saxicolous species in addition to a number of species treated as *Blastenia*. Doidge's list was compiled from literature and included many synonyms, thus a considerable reduction in the number of species should be expected in the planned new Lichen Flora of Southern Africa.

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Material

This work is based on material collected during fieldwork in South Africa from January to March 1984, and on the larger collections of *Caloplaca* at the Lund Herbarium, collected by Almborn in southern Africa in 1953. I have also studied type material and other specimens from G, H, PRE, S, STE, TRH, and W.

The revision of *Caloplaca* is planned for inclusion in the first fascicle of the family Teloschistaceae for the Lichen Flora of Southern Africa.

Morphology

Structure of the thallus. The studied material includes several different morphological types: crustose thallus, cracked-areolate thallus, areolate thallus with marginal lobes, thallus formed of small lobes and with lobate margin, and subfruticose thallus.

Caloplaca subunicolor is characterized by a very thin crustose thallus (Fig. 1a). In *C. almbornii* Kärnef., the thallus is composed of scattered areoles (Fig. 2b). *Caloplaca cinnabarina* and *C. haematodes* are variable. The thallus can be cracked-areolate to more distinctly areolate with marginal lobes (Fig. 1b). Material of these species may therefore be included in either of the two unnatural sections *Caloplaca* or *Gasparrinia* (Alon & Galun, 1971; Wade, 1965).

Caloplaca isidiosa, C. ochraceofulva, and *C. sublobulata* are characterized by more or less lobate thalli (Fig. 3). *Caloplaca elegantissima* differs from the other species in the cartilaginous, distinctly effigurate lobes (Figs. 4b, 5a). *Caloplaca bonae-spei,* in addition, differs from the other species in the subfruticose structure of the thallus (Fig. 5b).

Isidia. Asexual reproductive strategies are known in *Caloplaca isidiosa* and in *C. ochraceofulva. Caloplaca isidiosa* has rather elongate or coralloid isidia, while isidia in *C. ochraceofulva* are granular and concentrated on the margins of the squamulose areoles.

Pseudocyphellae. Larger portions of the dorsiventral lobes in *Caloplaca bonae-spei* are dominated by pseudocyphellae. Poelt & Pelleter (1984) stated that *C. elegantissima* was characterized by marginal pseudocyphellae at the base of the effigurate lobes. In my opinion, the white stripes occasionally seen at the base of the lobes are caused by exposure of the ecorticate basal parts (Fig. 5a).

Pigmentation. Color is variable in a few species, especially in *Caloplaca cinnabarina.* In the southernmost Cape Province the thallus is normally orange-red, but to the north, individuals are a paler color. I have studied this color variation within populations together with the morphological variation and concluded that it is correlated with the large climatic variation that occurs within its range. *Caloplaca almbornii* and *C. haematodes* have characteristically bright reddish pigments, while the other species are orange to yellowish. *Caloplaca elegantissima* has a characteristic orange-red pigmentation.

Anatomy

Caloplaca almbornii, C. cinnabarina, C. haematodes, C. isidiosa, C. ochraceofulva, and *C. sublobulata* are characterized by cortical layers composed of anticlinal paraplectenchymatous cells lying over a relatively dense medullary layer with interspersed, mainly clustered algae (Fig. 6a). This arrangement corresponds to the structure described in *C. granulosa, C. saxicola, C. scopularis,* and *C. verruculifera* by Poelt & Romauch (1977). A lower cortical layer as reported in *C. scopularis* was not observed.

Caloplaca elegantissima differs from the other species in having a relatively thick prosoplectenchymatous cortical layer lying over a thin pigmented layer and a very dense medullary layer. The clustered algae are basally arranged (Fig. 6b). This remarkable anatomical structure is presumably an adaptation to the extreme environmental conditions in the Namib coastal desert where it occurs.

Caloplaca bonae-spei also differs anatomically from the other species examined in having a cortical layer composed of periclinal hyphae lying over a dense medullary layer and interspersed clustered algae. The internal portion of the layer is filled with massive colorless, crystalline structures (Poelt & Pelleter, 1984).

Reproductive Structures

Apothecia. Apothecia are frequent in all species studied except *Caloplaca isidiosa* and *C. ochraceofulva.* In *C. almbornii, C. cinnabarina,* and *C. haematodes* apothecia are at first distinctly immersed, but they tend to become raised later in development (Figs. 1b, 2a). A distinct thalline margin or amphithecium, usually containing numerous algae, is developed in these three species and also in *C. isidiosa, C. ochraceofulva,* and *C.*

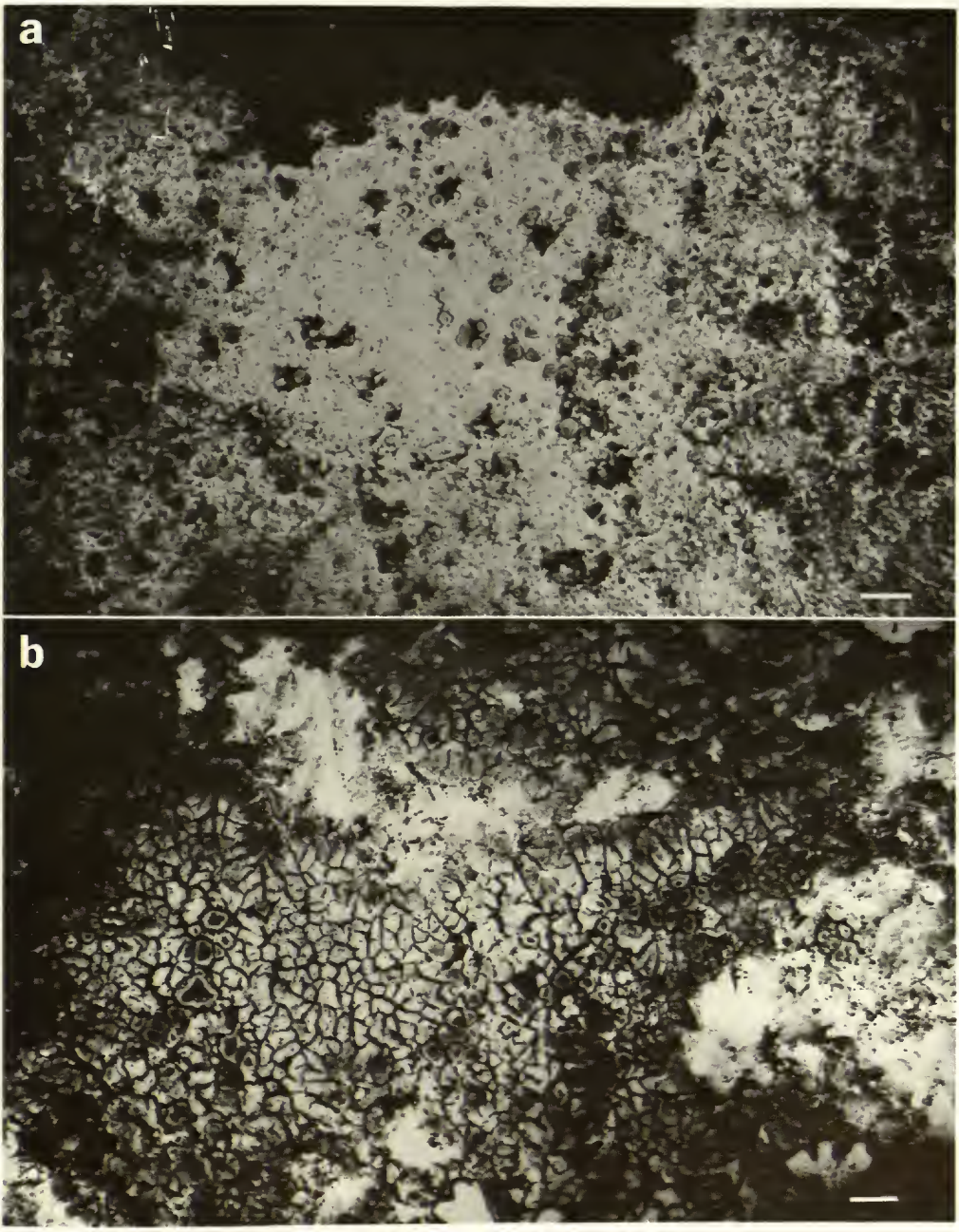

FIGURE 1.—a. Thin crustose thallus. *Caloplaca subunicolor,* S. A., Cape, Kirstenbosch, *Almborn 1430* (LD).—b. Cracked-areolate thallus. *C. cinnabarina,* S. A., Cape, Namaqualand, *Almborn & Kärnefelt 8417-21* (LD). Scales = 1 mm.

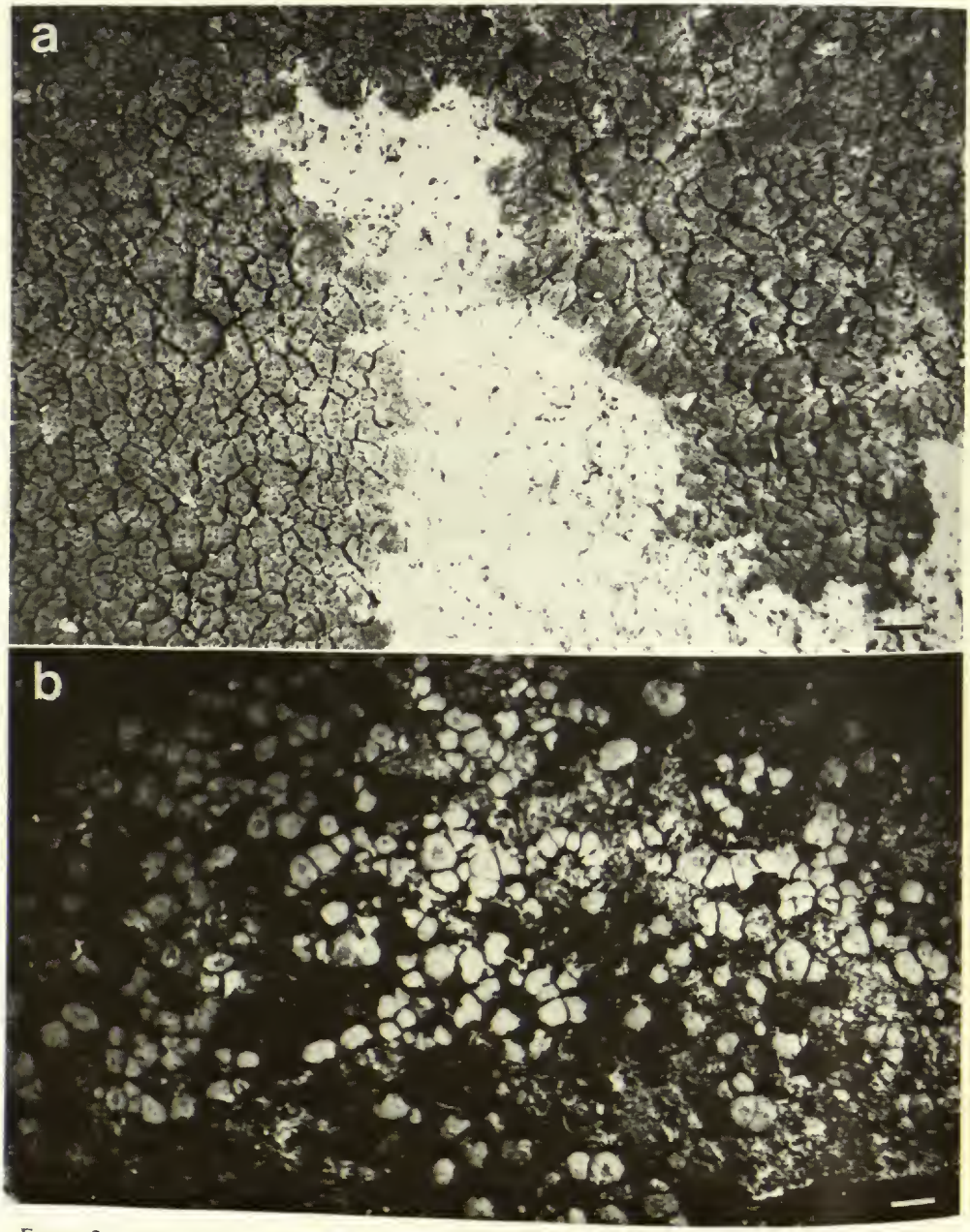

FIGURE 2.—a. Cracked-areolate thallus. *Caloplaca haematodes*, S. A., Cape, Prince Albert, *Marloth 1521* (PRE).—b. Thallus composed of scattered areoles. *C. almbornii*, Lesotho, Qachas Nek, *Koefler 1963* (LD). Scales = 1 mm.

sublobulata. A thin excipulum composed of vertical hyphae is present in several species (Fig. 7). *Caloplaca bonae-spei*, *C. elegantissima*, and *C. subunicolor* have lecidine apothecia with no distinct thalline margin developed.

The elongate asci correspond to the structure described by Honegger (1978, 1982) for Teloschistaceae. The ascospores are more or less ellipsoidal, polarilocular with two loculi, separated by a septum, and connected by a narrow canal.

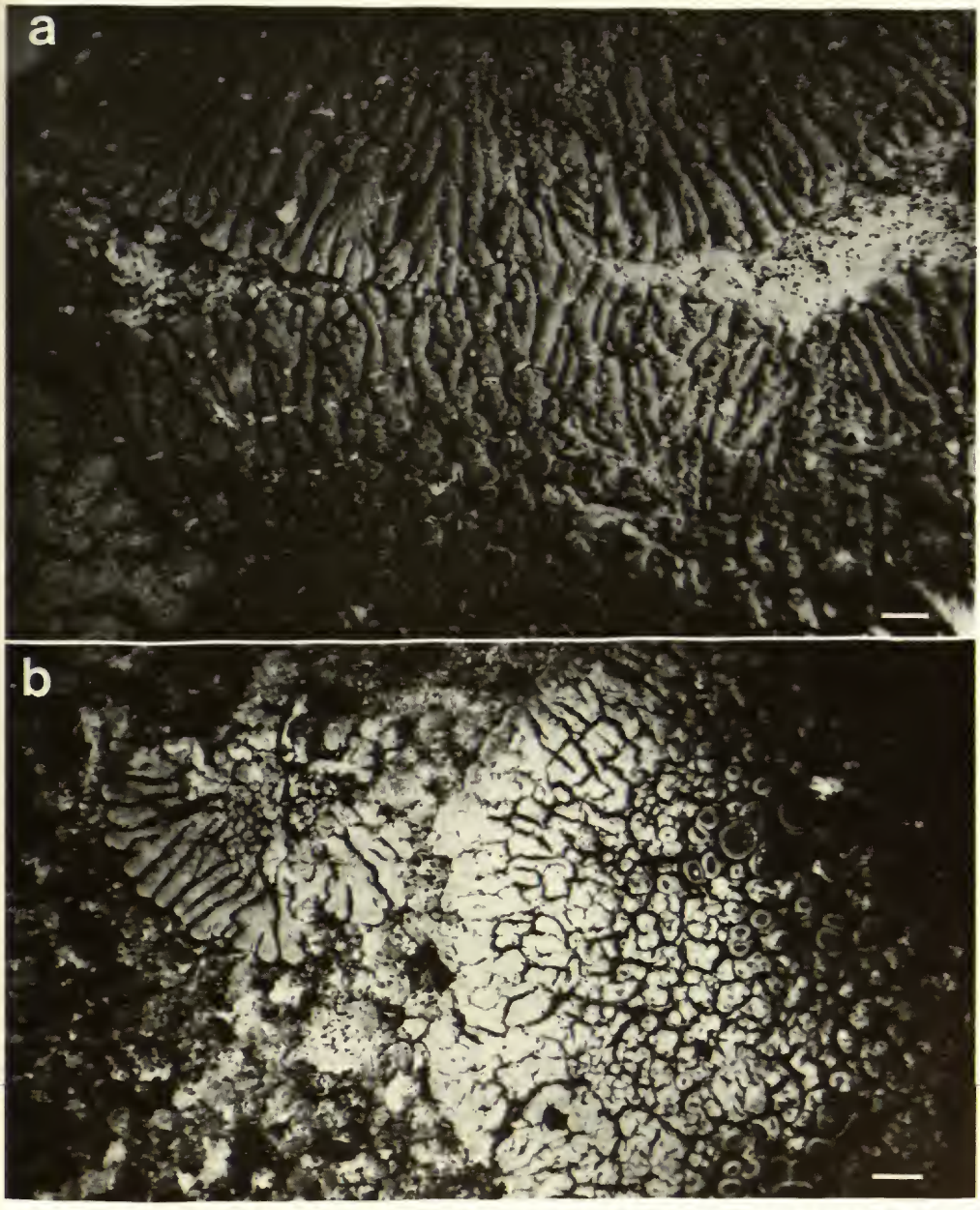

FIGURE 3.—a. Effigurate marginal lobes in *Caloplaca isidiosa* (top) and *C. sublobulata* (below). S. A., Cape, Simonstown, Pegrams Point, *Almborn & Kärnefelt 8410-3* (LD).—b. Specimens of *C. sublobulata* with effigurate marginal lobes (left) and thin palmate marginal lobes (right). S. A., Cape, Kommetjie, *Almborn Lich. Africani 48* (LD). Scales = 1 mm.

In *Caloplaca cinnabarina* there is a particularly large variation in spore size, but the most extreme spore sizes measured did not correlate with any other characters. The paraphyses are normally septate and apically branched. *Caloplaca bonae-spei* differs in having paraphyses with characteristic thickened apical cells containing oil (Poelt & Pelleter, 1984).

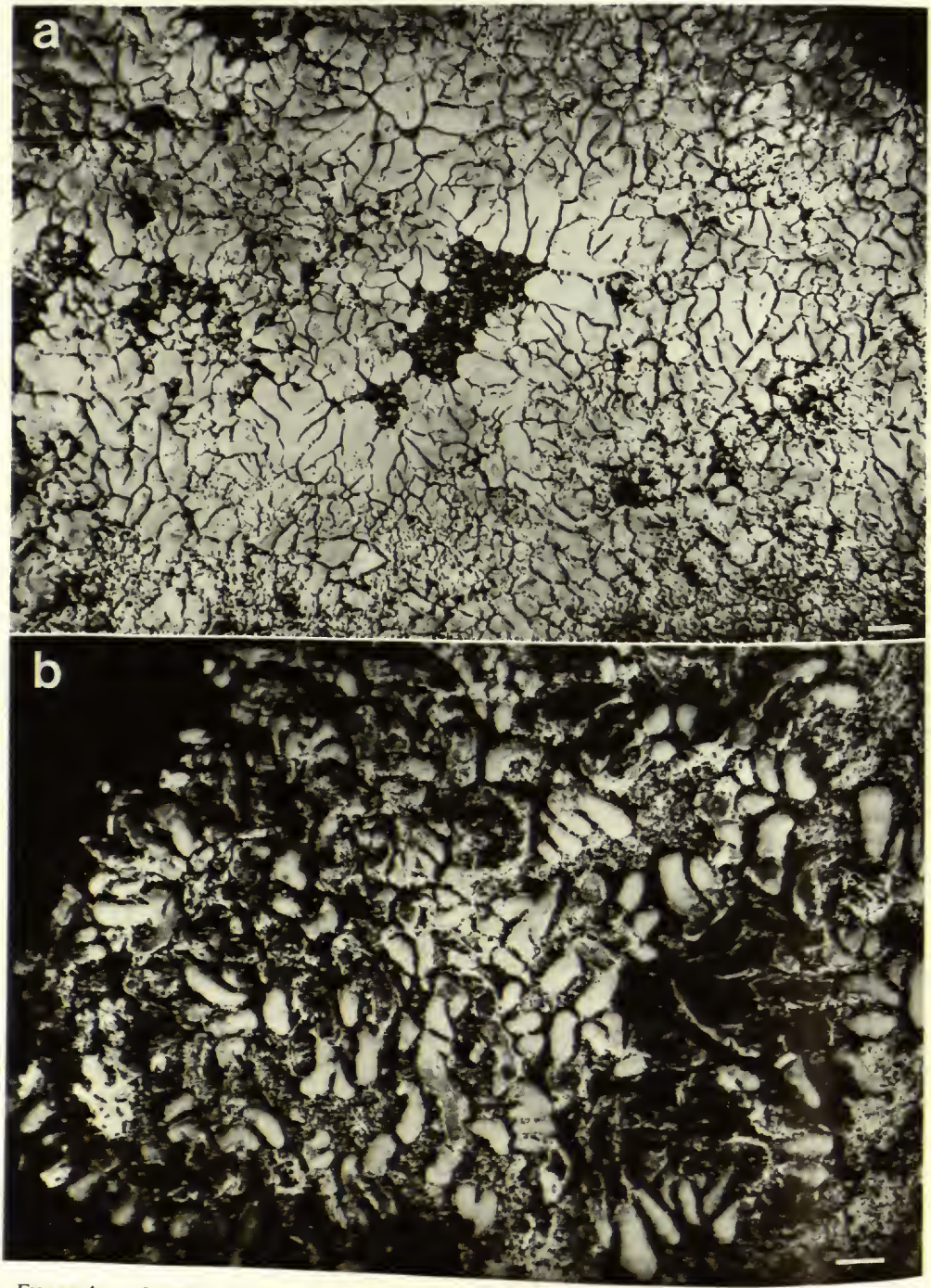

FIGURE 4.—a. Thallus with more or less squamulose areoles; isidia are seen as small granules. *Caloplaca ochraceofulva*, Lesotho, Leribe, *Koefler* (LD).—b. Central thallus portion of *C. elegantissima* with short irregular lobes. Namibia, Swakopmund, 25 km N of Henties Bay, *Nordenstam & Lundgren 2317* (S). Scales = 1 mm.

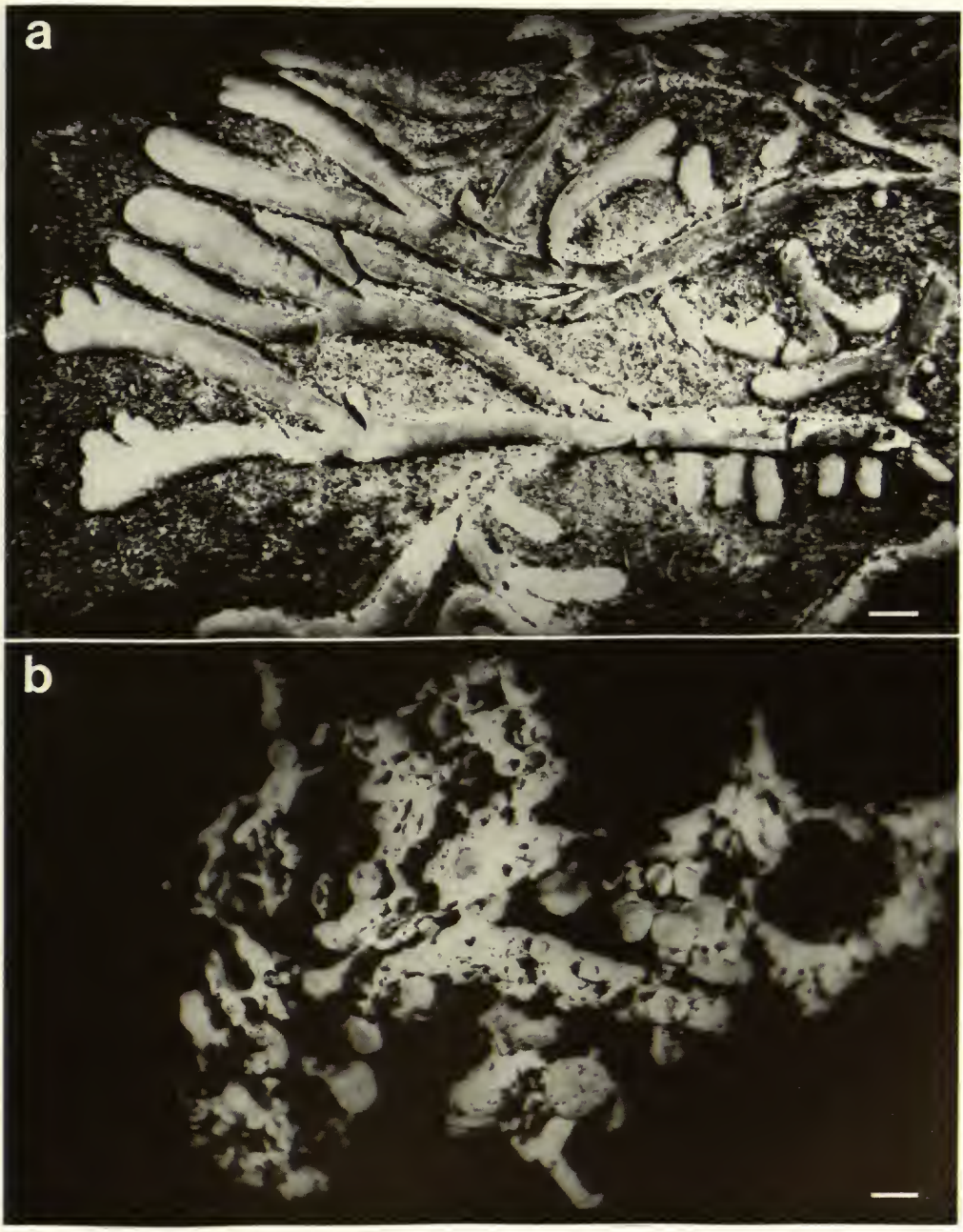

FIGURE 5.—a. Thallus composed of long effigurate lobes; note the marginal lobules. *Caloplaca elegantissima*, Namibia, Swakopmund, 25 km N of Henties Bay, *Nordenstam & Lundgren 2317* (S).—b. Subfruticose lobes in *C. bonae-spei*, S. A., Cape, Vanrhynsdorp, Strandfontein, *Almborn & Kärnefelt 8414-4* (LD). Scales = 1 mm.

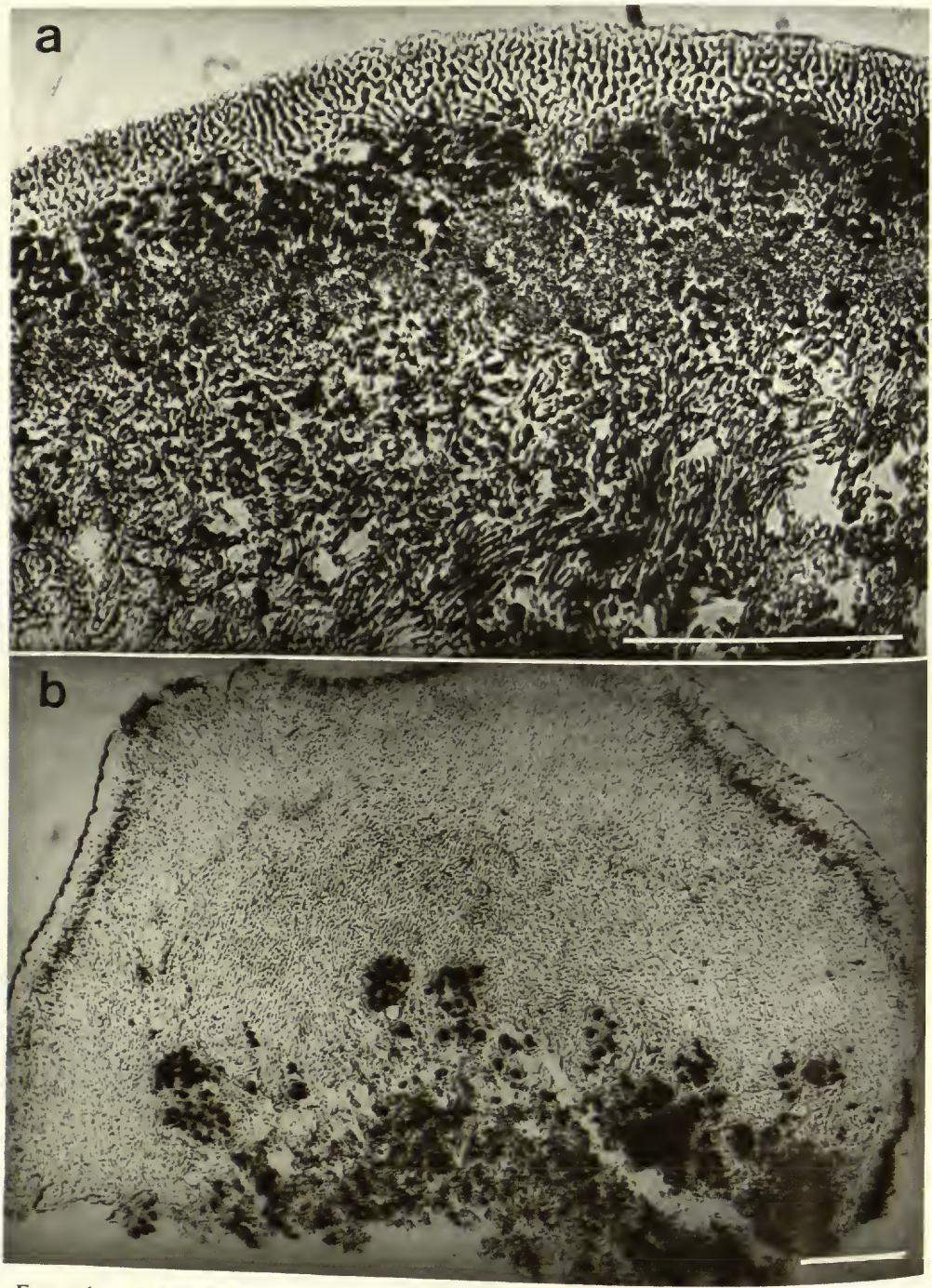

FIGURE 6.—a. Cortical layer composed of anticlinal paraplectenchymatous cells lying over the algae and a rather dense medullary layer. *Caloplaca cinnabarina*, S. A., Cape, Namaqualand, S of Kamieskroon, *Almborn & Kärnefelt 8417-27* (LD).—b. Prosoplectenchymatous cortical layer lying over a dense medullary layer and basal algae. *C. elegantissima*, Namibia, Swakopmund, *Desmond 25, 276* (LD). Scales = 100 μm.

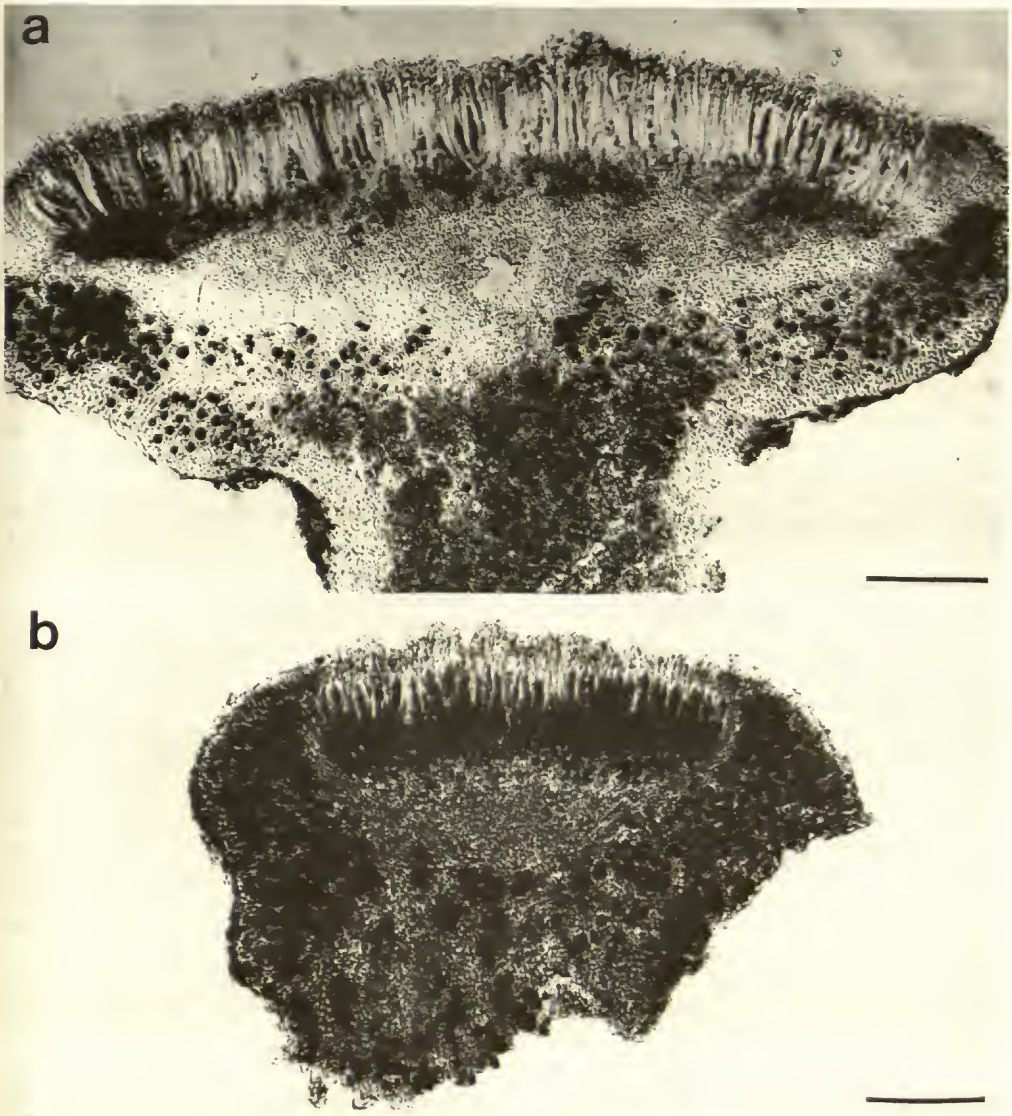

FIGURE 7.—a. Lecanorin apothecium in *Caloplaca sublobulata*, showing hymenium with pigmented epihymenial layer, hypothecium, excipulum, and amphithecium with algae. S. A., Cape, Bakoven, *Almborn & Kärnefelt 849-2* (LD).—b. Lecanorin apothecium in *C. cinnabarina*. S. A., Cape, Namaqualand, 30 km S of Kamieskroon, *Almborn & Kärnefelt 8416-27* (LD). Scales = 100 μm.

Pycnidia. Pycnidia have been observed in *Caloplaca bonae-spei* and in *C. sublobulata*. Poelt & Pelleter (1984) referred to these structures as spermogonia and indicated their male sexual function. True asexually functioning pycnidia are not, according to Poelt & Pelleter (1984), developed within Teloschistaceae. Their function may be in sexual reproduction only, but since they seem to be absent in the majority of species, the neutral term pycnidium is more appropriate. It was rather striking, however, to observe the abundance of pycnidia in populations of *C. sublobulata* and the complete absence of pycnidia in the closely associated *C. isidiosa*. The pycnoconidia (spermatia) are very small and rod-shaped.

Chemistry

The chemistry has been investigated in detail in many species by Santesson (1970) and Steiner & Hauschild (1970). Santesson, who investigated ca. 230 species by means of lichen mass spectrometry (LMS) and TLC, found several closely related anthraquinones, i.e., emodin, parietin, teloschistin (as fallacinol), and/or xanthorin, and/or erythroglaucin, and fallacinal in *Caloplaca bonae-spei* (as *C. regalis*), *C. haematodes, C. isidiosa* (as *C. granulosa*), *C. ochraceofulva* (as *C. subnitida*), and *C. sublobulata. Caloplaca cinnabarina* and *C. elegantissima* (the last examined by Steiner & Hauschild, 1970) in addition contained parietinic acid, while *C. subunicolor* lacked emodin. Santesson (1970) also examined isotype material of *C. isidiosa* from Brazil, which contained emodin, parietin, and fragelin, being slightly different from a South African population.

Geographical Variation

Caloplaca cinnabarina and *C. sublobulata* are the most variable of the saxicolous species in southern Africa. Several segregates have been described, for example, by Zahlbruckner (1932, 1936), who recognized local forms at specific rank based on material he had not seen in the field. In South Africa I observed an interesting geographical variation within *C. cinnabarina.* In the southernmost Cape Province this species has a rather smooth cracked-areolate orange-red thallus with immersed apothecia. To the north towards Namaqualand more distinct areoles and marginal lobes are developed, the apothecia become more raised, and the color paler. A similar pattern was also observed in the closely related *C. haematodes.* Local extreme forms with large areoles and pale colors appear very distinct when studied alone, but in the field it is not possible to separate these from numerous intermediate morphotypes and color variants.

Caloplaca sublobulata comprises two extreme morphotypes on coastal rocks in South Africa. One has characteristically effigurate lobes and the other very thin, palmate marginal lobes (Fig. 3b), but in nearby large populations a number of intermediate forms also occur. A similar variation has been described from populations of *C. sublobulata* in southernmost South America (Santesson, 1944).

Widespread lichen species are in general more variable than species with more limited ranges since they must adapt to different environmental and climatic conditions. The obvious morpholgoical variation within *Caloplaca cinnabarina* is presumably also correlated with climatic differences in southern Africa (Werger, 1978). The morphological variation in *C. sublobulata* may be a result of different exposure and habitat selection on the coastal rocks.

Biogeography

Four species are endemic to southern Africa: *Caloplaca almbornii,* known from a few localities at high elevations in the eastern Cape Province and Natal, Lesotho and Zimbabwe (Fig. 8a); *C. bonae-spei,* known from coastal rocks in western Cape Province (Fig. 8b); *C. haematodes,* known mainly from the western Cape Province and the Orange Free State (Fig. 8d); and *C. elegantissima* from the coastal Namib desert in Namibia and southern Angola (Fig. 8c).

Caloplaca ochraceofulva and *C. subunicolor* occur mainly in southern Africa but are also known from a few localities in South America. *Caloplaca ochraceofulva* is more widespread, known from high elevations in the Cape Province, Orange Free State, and Natal, Namibia, Lesotho, Kenya, and Somaliland (Fig. 9b). *Caloplaca subunicolor* is most frequent in the Cape Province but also occurs in Zimbabwe (Fig. 9c). Materials of the two transatlantic populations of these species are morphologically very similar.

Caloplaca isidiosa is known from the southernmost Cape Province on coastal rocks and from a few localities in western Brazil and in the Galápagos Islands (Fig. 9a). The South African population of *C. isidiosa,* however, differs slightly from the limited material seen from Brazil, which has more granular isidia. The specimen from the Galápagos Islands is more reminiscent of South African specimens. It is possible that after a detailed study of material from South America, the species may be treated as representing two geographically isolated taxa. These two predominantly asexually reproducing species have an African–South American distribution which is otherwise not common among the lichens. Asexual distribution in clones over wide areas is advantageous in lichens, but I doubt it is the case here. The possible evolution and dispersal of an ecologically different species, *Coelocaulon epiphorellum,* which occurs mainly in southernmost South America and in South Africa, has been recently discussed by Kärnefelt (1986).

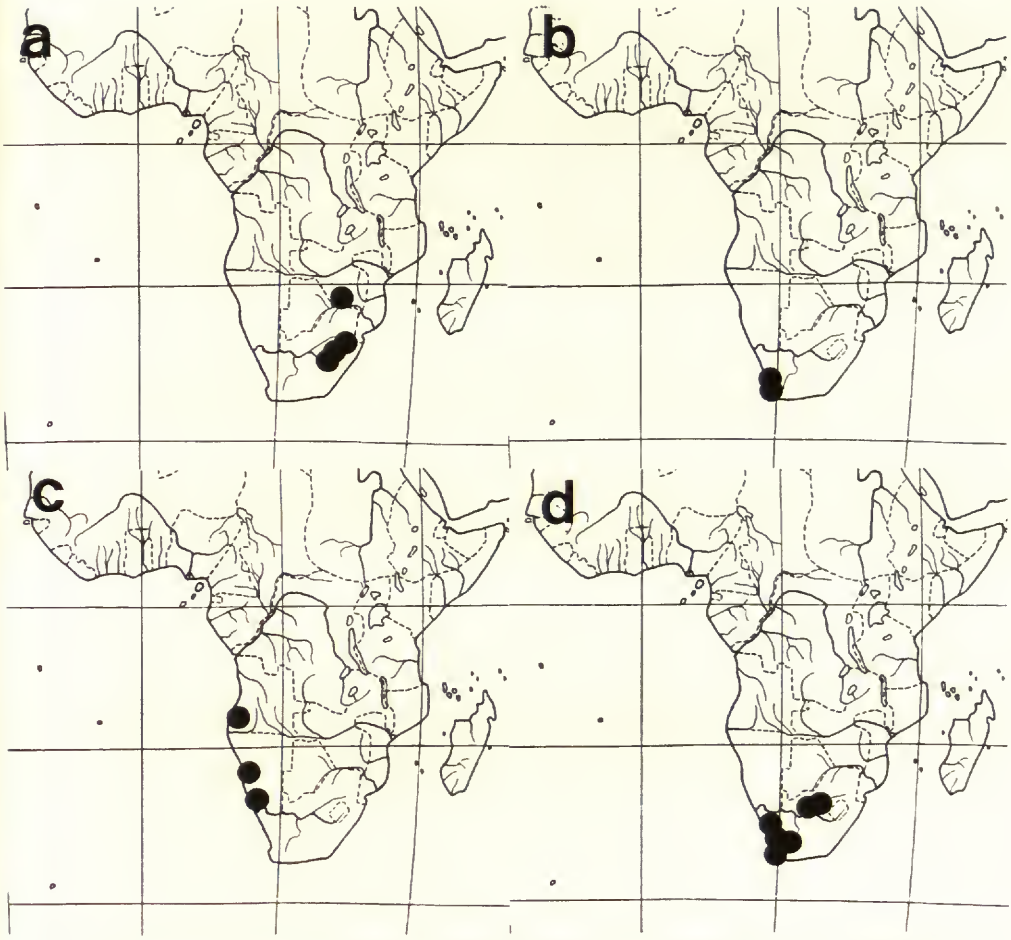

FIGURE 8. Endemic species of *Caloplaca* in southern Africa.—a. *C. almbornii*.—b. *C. bonae-spei*.—c. *C. elegantissima*.—d. *C. haematodes*.

Caloplaca sublobulata is locally common along the southern coast of Cape Province to Natal in South Africa, in southernmost South America, and adjacent subantarctic islands (Fig. 10b). It is also recorded from New Zealand and South Australia (Santesson, 1944). There appear to be some minor differences in morphology and pigmentation between the two major population centers in South Africa and South America, but these differences cannot be evaluated taxonomically at present.

Caloplaca cinnabarina is the most widely distributed species in southern Africa and in other tropical and subtropical regions as well (Fig. 10a). It is found from coastal sites in the Cape Province to higher elevations throughout South Africa, Lesotho, Swaziland, Mozambique, Zimbabwe, Ivory Coast, and Guinea on the African continent.

AFFINITIES

Caloplaca cinnabarina and *C. haematodes* appear to be closely related species. Especially within the Cape Province they exhibit a similar morphological variation, and both species have adapted to similar habitats. There is, however, a slight difference in pigmentation and chemical content. *Caloplaca almbornii* is apparently related to *C. haematodes* in pigmentation and also in the structure of apothecia, but differs in the scattered areoles.

Caloplaca sublobulata and *C. isidiata* are

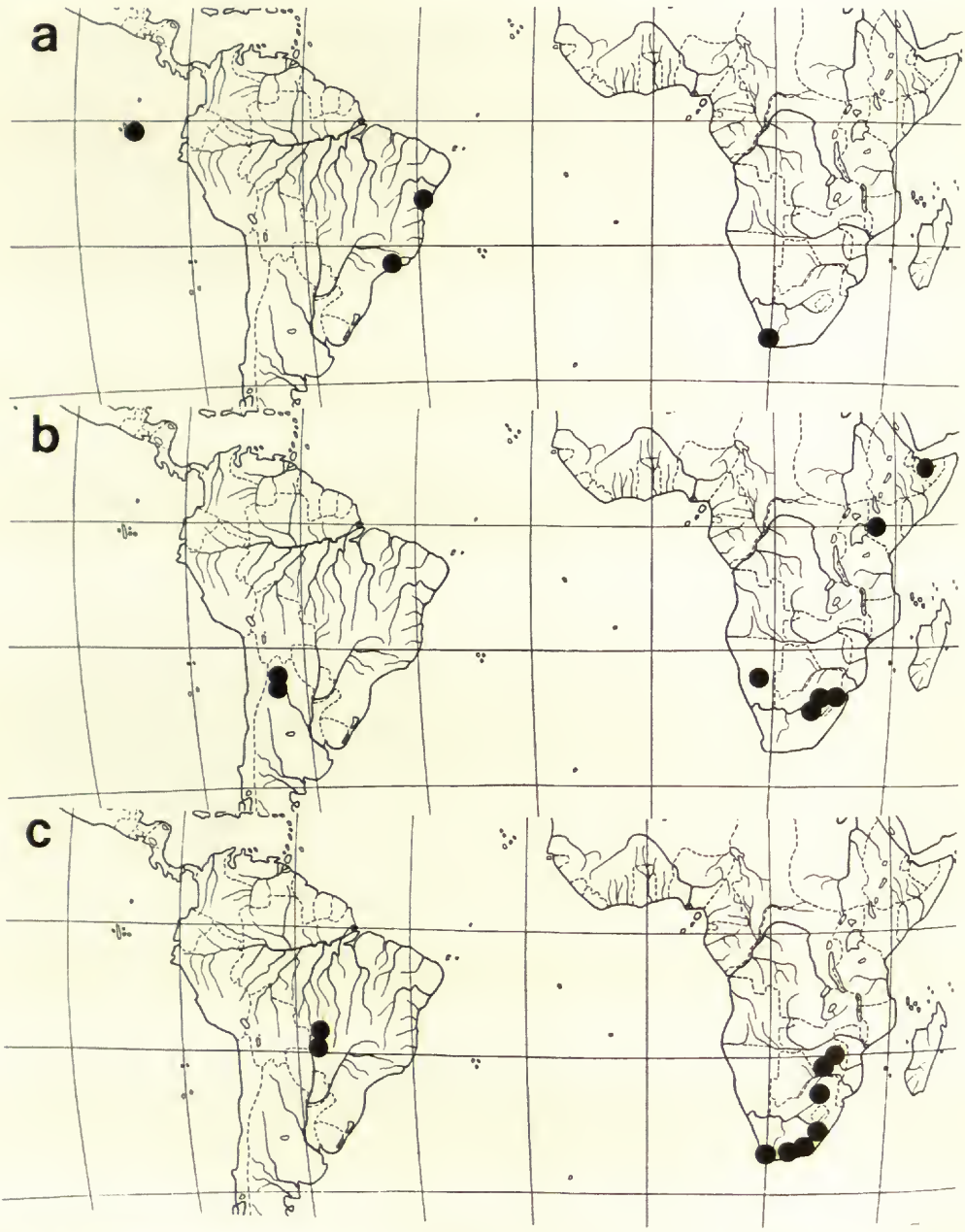

FIGURE 9. African–South American species of *Caloplaca*.—a. *C. isidiosa*.—b. *C. ochraceofulva*.—c. *C. subunicolor*.

closely related and form a species pair in South Africa, where *C. sublobulata* is the primary species, with normal reproduction, while the secondary species mainly reproduces in clones. They differ only in reproductive characters. Since the secondary species occasionally develops apothecia, is less frequent, and has a limited distribution, I assume it is still in the process of evolving into a better-adapted apomictic species.

In the Northern Hemisphere *Caloplaca ma-*

FIGURE 10. Widespread Southern Hemisphere species (material from Australia and New Zealand not seen).—a. *C. cinnabarina*.—b. *C. sublobulata*.

rina and *C. littorea,* which is the asexual isidiate counterpart of *C. marina,* may represent a vicariant species pair with *C. sublobulata* and *C. isidiosa.*

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THE BRYOFLORA OF NAMIBIA[1]

S. RUSSELL[2] AND J. VAN ROOY[3]

ABSTRACT

A total of 93 bryophyte species have so far been collected in South West Africa/Namibia, of which 10 species are endemic to the region. The bryoflora is dominated by xeromorphic mosses and a large group of xerophytic thalloid liverworts occurring especially in protected niches in montane habitats. Ephemerals and species that are thought to rely on mist precipitation for survival also occur in desert habitats. Pleurocarpous mosses are rare and confined to "oases" of relatively well-watered dry woodland, and no leafy Hepaticae have yet been recorded for the region. Further collecting, especially in the more easterly, higher rainfall areas, is expected to add to the number of species of both mosses and liverworts listed for the region. The physiology of the many common desiccation-resistant thalloid liverworts is deserving of further study.

RÉSUMÉ

Sur les 93 espèces de bryophytes récoltées jusqu'à présent en Afrique du Sud-ouest/Namibie, 10 sont endémiques à cette région. La bryo-flore est dominée par des mousses xéromorphes et par un groupe important d'hépatiques à thalle xérophytes qui se trouvent tout particulièrement dans des niches protégées d'habitats de montagne. Dans des habitats désertiques se trouvent les espèces éphémères et celles qui, pense-t-on, dépendent des rosées pour leur survie. Les mousses pleurocarpes sont rares et confinées dans les "oasis" de régions boisées arides relativement bien arrosées et on n'a pas encore répertorié d'hépatiques à feuilles dans cette région. De nouvelles récoltes, surtout dans les régions les plus orientales où la précipitation est élevée, devraient permettre d'accroître le nombre d'espèces de mousses et d'hépatiques répertorié pour cette région. La physiologie de nombreuses hépatiques à thalle qui résistent à la déssiccation merite d'être étudiée plus à fond.

Werger (1978) and Seely (1984) have commented on the richness and endemism of the Karoo-Namib vascular flora and its implications for paleoecological reconstructions. Schuster (1983) pointed out the ability of mosses and liverworts to survive in protected microhabitats "long after the general climate of a region has become 'inimical'," and he therefore suggested that the bryophytes "potentially offer a better clue to the solution of phytogeographical problems than do many vascular plants." It is therefore surprising that, despite the relative richness of the Namib lichen and liverwort floras (Schoeman, 1984; Scott, 1982), very few studies have so far been carried out on Namibian cryptogams. The following is an attempt to gather together what little is known concerning the Namibian bryoflora in the hope of stimulating further research in the group.

BRYOLOGICAL COLLECTING

Plant specimens in the herbarium at Zurich include bryophytes collected by Hans Schinz in Namibia as early as 1886. Schinz stayed for several months in Ovamboland with the Russian missionary Martti Rautanen, who made further collections from this area at the turn of the century. The independent collector Kurt Dinter also sent specimens to Schinz and continued to collect plants in SWA (including bryophytes) until the early 1930s.

Studies in European herbaria may reveal further bryophyte records resulting from the collections of German botanists during the 1930s. However, modern records of Namibian bryophytes known to the authors only begin with the collections of the amateur botanist J. Lavranos in the 1950s. Several bryophyte specimens were

[1] Acknowledgments are due to the South African Council for Scientific and Industrial Research and the South West Africa Administration, Department of Nature Conservation and Tourism for assistance with this project. Special thanks are also due to Dr. M. K. Seely for hospitality during the first author's stay at the Desert Ecological Research Unit at Gobabeb in the Namib Desert and to Mrs. S. V. Morrissey for typing and assistance with the figures.

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also collected by members of staff from the Botanical Research Institute in Pretoria during the 1960s and 1970s, e.g., H. Anderson, D. S. Hardy, J. Phelan, L. Smook, S. Venter, etc. W. Giess of the Windhoek herbarium made fairly extensive collections during this period, although the most prolific collector has been Dr. O. H. Volk, now at the University of Würzburg. Dr. Volk commenced botanical studies in Namibia in 1937 and has published several papers on the liverwort flora of the country, especially the genus *Riccia* (Volk, 1979, 1981, 1984a, 1984b). Most specimens of namibian bryophytes are found in the herbaria at Zurich (Z), Berlin (B), St. Louis (MO), Windhoek (WIND), and Pretoria (PRE).

Bryophyte Diversity and Distribution

The preliminary bryophyte species list presented here (see Appendix I) is based on a PRECIS computer printout (Magill et al., 1983) of specimens in the cryptogamic herbarium at the Botanical Research Institute in Pretoria (incorporating regional herbaria). Specimens in the bryological collection of the Plant Sciences department at Fort Hare University and recent hepatic records of Dr. O. H. Volk have also contributed to the list.

A recent analysis of plant collecting intensity in southern Africa using the PRECIS data base (Gibbs Russell et al., 1984) revealed that Namibia has been very poorly collected, with less than 50 specimens recorded from 90% of its quarter degree grid squares. Bryophytes have been particularly neglected, with only 96 taxa recorded so far for the 823,000 km^2 region.

According to the list, several major groups of bryophytes appear to be missing from the Namibian flora, e.g., the Jungermanniales (leafy liverworts) and most families of the large moss orders Isobryales, Hookeriales, and Polytrichales. Until research for this paper commenced, there were no published records of pleurocarpous mosses (more than a third of southern African species) for the entire country. Among those species which have been collected are many xerophytic thalloid liverworts. The flora is also rich in xeromorphic mosses, especially of the family Pottiaceae. The lack of collecting is emphasized by concentration of the few existing records along major roads and around population centers (e.g., Windhoek, where the country's principal herbarium is situated; Fig. 1).

Although influenced by the restricted collecting pattern, distribution of bryophytes in Namibia shows a limited degree of correlation with macroenvironmental features. Records cluster around areas of high ground (e.g., Waterberg Plateau, Windhoek Highlands, Nankluftberge, and Karasberg; Fig. 2). Shaded cliff-face niches, cooler temperatures at higher altitude, and orographic rainfall may account for this pattern (see Ecological Notes). The correlation of distribution with rainfall is less obvious (Fig. 3), although improved collecting in the east may alter this picture.

Biogeographical Notes

Percentages of Namibian bryophyte species showing distinctive distribution patterns are given in Table 1. Of the 93 species listed for Namibia, 13 are typical of semiarid and savannah habitats in eastern and southern Africa. Thirty-one species, including the bulk of the xerophytic liverworts, are endemic to Africa south of the Zambezi (33%). This compares with 22% southern African endemism in the forest bryoflora of the eastern Cape, for example (Russell & Van Rooy, in press).

Bryophytes are more common in the eastern, higher rainfall areas of Namibia. These areas have more in common floristically with the Kalahari and semiarid regions of South Africa, and strict endemism within the political unit of Namibia is therefore relatively low amongst the bryophytes (10 species). Further collecting and taxonomic work may, however, alter this proportion significantly. In the relatively well-studied genus *Riccia,* for example, 37% of the species are currently thought to be endemic to Namibia.

In the Namib region the extreme climatic conditions restrict the bryoflora to those species with broad ecological tolerances. Eight of the 17 species so far recorded from this region are typical cosmopolitan or very widespread taxa.

Among those species showing disjunct or anomalous distributions, *Barbula crinita* and *Campylopus introflexus* have a predominantly Southern Hemisphere range. *Trichostomopsis australasiae* also has a wide distribution but is not found in Eurasia, while *Riccia crystallina* is found widely in the Northern Hemisphere with an outlier in southern Africa. *Tortula porphyreoneura* and *Archidium microthecium* have southern African distributions with extensions through East Africa into Asia. *Riccia perssonii*

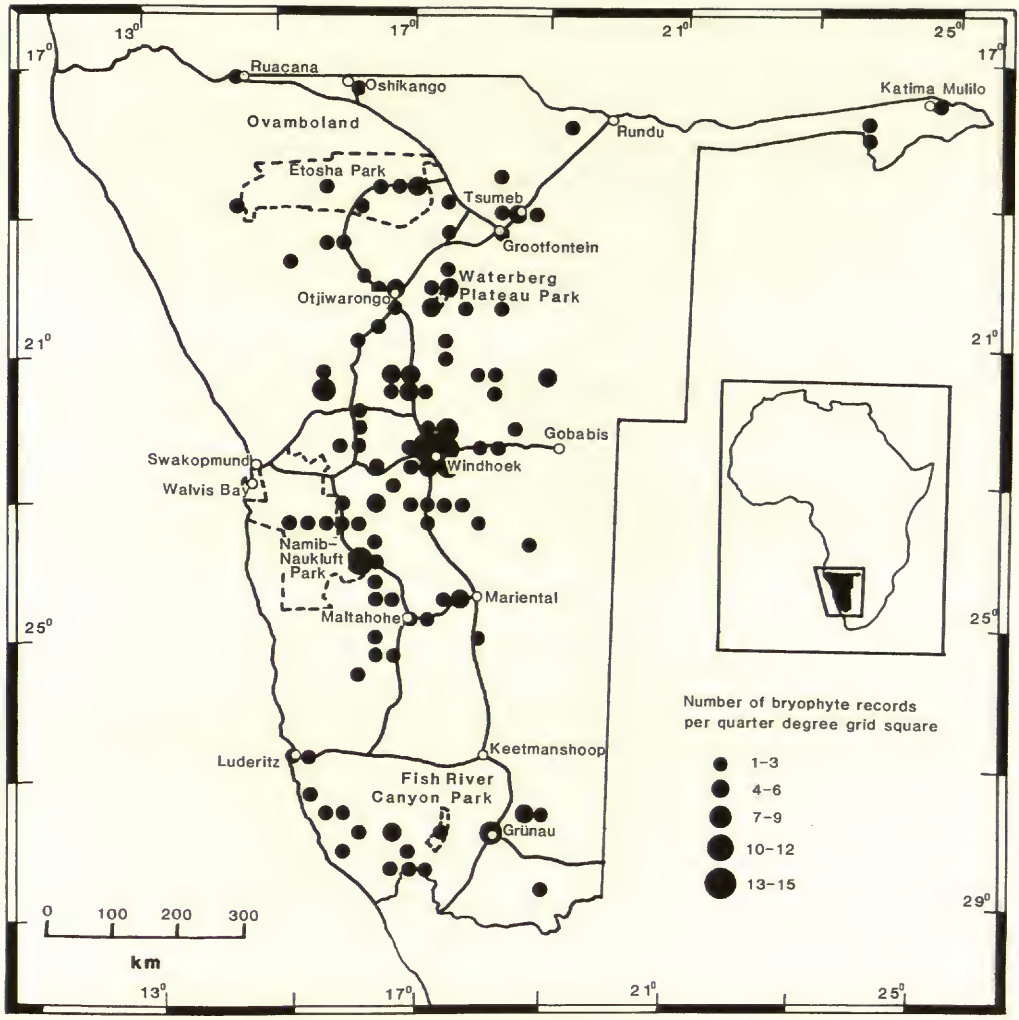

FIGURE 1. Distribution of bryophytes in Namibia in relation to roads and population centers.

and *Brachymenium acuminatum* have distributions disjunct between SWA/Namibia and Pakistan, and southern Africa and India/Indonesia, respectively. *Plagiothecium rhynchostegioides* has been found only in southern Africa and China/Japan.

Bryum cellulare, B. nitens, and *B. radiculosum* have African/Asian distributions with extensions into Europe, and a group of four hepatic species shows links between southern Africa and the Mediterranean/European region, with outliers on African islands (e.g., *Exormotheca pustulosa, Athalamia spathysii, Riccia canescens,* and *R. crozalsii*). A further two species show distributions disjunct between southern Africa and the Americas, viz. *Symphyogyna podophylla* and *Tortula ammonsiana,* while *Gigaspermum repens* has only been recorded from southern Africa and Australasia. *Archidium ohioense* has been found sporadically in North America, the West Indies, Africa, India, and Japan.

ECOLOGICAL NOTES

Mosses and liverworts tend to be thought of as plants confined to continuously damp habitats. Scott (1982), however, pointed out that these simple plants are potentially better adapted for

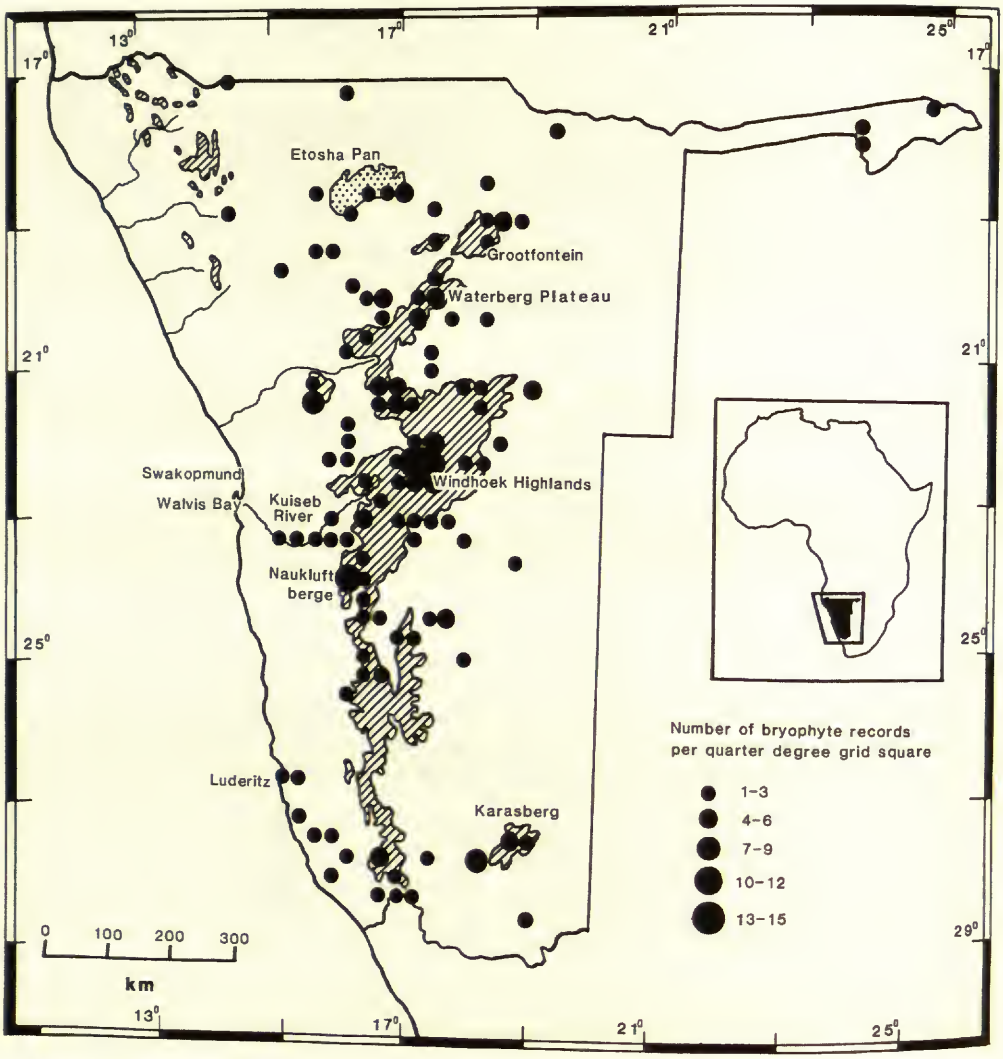

FIGURE 2. Distribution of bryophytes in Namibia in relation to altitude (shaded area denotes terrain above 1,500 m).

survival in conditions of extreme drought than any other group of plants excepting perhaps the lichens. Many bryophytes are able to suspend metabolism during periods of drought, when their tissue water contents fall far below those at which most vascular plants perish. Unique protoplasmic properties allow desiccation-tolerant bryophytes to resume photosynthesis quickly whenever a rare rain shower or deposition of dew takes place in the desert environment (Oliver & Bewley, 1984).

Volk (1984b) suggested that forms of precipitation other than rain are necessary for survival of *Riccia* in Namibia wherever the rainfall is less than 150 mm per annum. The well-documented prevalence of fog and dewfall in the Namib may therefore help account for the existence of bryophytes in the drier western parts of the country, e.g., south of Luderitz (Fig. 3). Nagel (1962), for example, found an equivalent rainfall of 130 mm per annum derived from fog precipitation at Swakopmund (Fig. 3), where the actual mean annual rainfall measured conventionally totals only 18 mm. Several of the records from the arid western region are for bryophytes of periodically damp habitats such as banks of intermittently

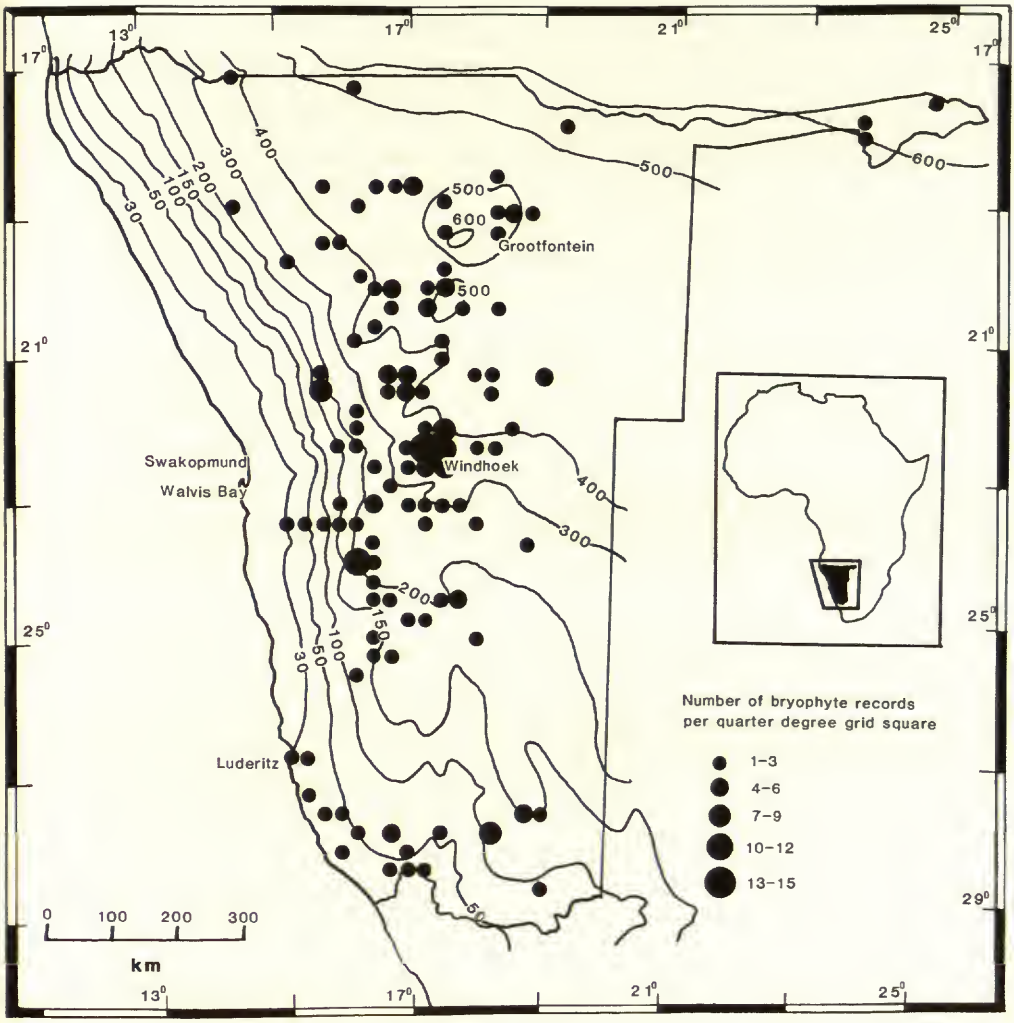

FIGURE 3. Distribution of bryophytes in Namibia in relation to rainfall (mean annual rainfall isohyets in mm).

flowing streams. An example is *Riccia cavernosa*, a fast-growing "opportunist" found along the course of the Kuiseb River (Fig. 2).

Most bryophytes in Namibia are found confined to clefts and crevices in rock outcrops, where runoff may be concentrated and protection from radiation provides an ameliorated microenvironment. The thalloid liverwort *Plagiochasma rupestre* and the moss *Desmatodon convolutus* are almost ubiquitous in such niches in the mountains of the Namib hinterland, especially on geological substrates that degrade to a fine, less easily drained soil.

Common xerophytic liverworts of such habitats include *Targionia hypophylla, Mannia capensis, Exormotheca pustulosa, Oxymitra cristata, Riccia canescens*, etc. These species tend to be characterized by a desiccation *avoidance* strategy during times of drought. Much of the marginal tissue may die off and the thallus often curls up to protect the sensitive growing point with a thick layer of pigmented ventral scales or cilia. Shiny or crystalloid crusts occur on the surface of several species and will also reflect radiation. The stem apex will therefore be protected from drying out and may withstand drought for long

TABLE 1. Biogeographical affinities of Namibian bryophytes.

Distribution	No. of Species	% of Total Bryo-flora
Cosmopolitan	6	7
Widespread	14	15
Southern and Eastern Africa	13	14
Southern Africa	31	33
SWA/Namibia endemic	10	11
Disjunct/anomalous	19	20
Total	93	100

periods [up to seven years has been recorded in the case of *Riccia canescens* (Volk, 1984b)].

The mosses, on the other hand, tend to exhibit a desiccation tolerance strategy, with tissue water potentials as low as −300 MPa (equivalent to 5% tissue water content) having been recorded in revivable specimens of *Trichostomum brachydontium* (Russell, unpubl. data). Features such as the incurling of leaves, hyaline hair points, the occurrence of shading filaments and lamellae on leaf surfaces, papillose cell walls, etc., are all thought to be adaptations to withstand the desert radiation regime (Scott, 1982). Common examples of xeromorphic mosses occurring in Namibia include *Desmatodon convolutus, Barbula crinita, Tortula porphyreoneura, Trichostomum brachydontium,* and *Bryum argenteum.*

Several minute mosses of ephemerally damp environments such as pans also occur. Examples are *Archidium dinteri, Chamaebryum pottioides, Gigaspermum repens,* and *Physcomitrium spathulatum.*

D. Gaff (in Scott, 1982; pers. comm.) reports bryophytes occupying the specialized microhabitat beneath translucent quartz boulders in the Namib Desert. This niche often supports rich growths of cyanobacteria (pers. obs.). Shaded sites at which a permanent water supply exists, such as caves and springs beneath cliffs in the eastern areas of Namibia, may support thick carpets of species such as *Philonotis dregeana, Campylopus bequaertii, Plagiothecium rhynchostegioides,* and the desiccation-sensitive liverwort *Symphyogyna podophylla.* At Grootfontein and the Waterberg Plateau, where the higher rainfall allows a dense woodland to develop, pleurocarpous mosses may be found growing epiphytically on tree bark (e.g., *Erpodium transvaaliense, Fabronia leikipiae, Lindbergia* sp.). These species are also found in dry woodland in neighboring regions of southern Africa and are not typical of the moister eastern forests of the subcontinent.

CONCLUSION

Mosses and liverworts are widespread in Namibia, but poorly collected. Existing records show the influence of population centers and roads on collecting frequency, but correlations of bryophyte distribution with macroenvironmental features such as altitude and precipitation are also emerging. Most bryophytes are found in protected microhabitats in the more mountainous regions of the country. The survival of some species in the low rainfall areas closer to the coast is probably associated with the occurrence of fog precipitation.

With the limited information available, it is not possible to affirm a relictual origin for the mesophytic bryophytes occurring in pockets of higher rainfall woodland in eastern Namibia. The spectrum of species so far collected argues against the proposal of refugium status for these "bryological oases."

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APPENDIX I

Preliminary checklist of SWA/Namibia bryophytes. Families are arranged according to the sequence in Magill & Schelpe (1982).

HEPATICAE

Targioniaceae (H1)
Targionia hypophylla L.

Aytoniaceae (H2)
Grimaldia sp.
Mannia capensis (Steph.) S. Arnell
Plagiochasma beccarianum Steph.
P. microcephalum (Steph.) Steph.
P. rupestre (Forst.) Steph.

Exormothecaceae (H4)
Exormotheca holstii Steph.
E. megastomata Marquand
E. pustulosa Mitt.

Cleveaceae (H5)
Athalamia spathysii (Lindb.) Hatt.

Oxymitraceae (H7)
Oxymitra cristata Garside

Ricciaceae (H8)
Riccia albolimbata S. Arnell
R. albosquamata S. Arnell
R. albovestita Volk
R. angolensis Steph.
R. atropurpurea Sim
R. canescens Steph.
R. cavernosa Hoffm. emend. Raddi
R. crozalsii Lev.
R. crystallina L. emend. Raddi
R. gemmifera Volk
R. limbatoides nom. prov.
R. okahandjana S. Arnell
R. perssonii Kahn
R. runssorensis Steph.
R. stricta (Trev.) Duthie
R. volkii S. Arnell

Riellaceae (H10)
Riella echinospora Wigglesw.

Codoniaceae (H11)
Fossombronia sp.

Pallaviciniaceae (H14)
Symphyogyna podophylla (Thunb.) N. & M.

Anthocerotaceae (A1)
Anthoceros natalensis Steph.
Phaeoceros laevis (L.) Prosk.

MUSCI

Fissidentaceae (3)
Fissidens capriviensis Magill
F. pseudoserratus (C. Muell.) Jaeg.
F. rufescens Hornsch.—no locality
F. subobtusatus C. Muell.

Archidiaceae (4)
Archidium dinteri (Irmsch.) Snider
A. microthecium Dix. & P. Vard.
A. ohioense Schimp. ex C. Muell.

Dicranaceae (8)
Bruchia foveolata Magill
Campylopus atroluteus (C. Muell.) Par.
C. introflexus (Hedw.) Brid.
C. pilifer Brid.
Cladophascum gymnomitrioides (Dix.) Dix.
Trematodon intermedius Welw. & Duby

Pottiaceae (14)
Barbula acutata C. Muell.
B. afrofontana (C. Muell.) Broth.
B. crinita Schultz
Crossidium spiralifolium Magill
Desmatodon convolutus (Brid.) Grout
D. longipedunculata (C. Muell.) Magill
Didymodon ceratodonteus (C. Muell.) Dix.
Gymnostomum aeruginosum Sm.
Husnotiella latifolia (Dix.) Zander & Magill
Hymenostylium recurvirostrum (Hedw.) Dix.
Pottia subplanomarginata Dix.
Tortella xanthocarpa (C. Muell.) Broth.
Tortula ammonsiana Crum & Anderson
T. longipedunculata (C. Muell.) Broth.
T. muralis Hedw.
T. porphyreoneura (C. Muell.) Towns.
T. ruralis (Hedw.) Gaertn., Meyer & Scherb.
T. torquatifolia (Geh.) Dix.
Trichostomopsis australasiae (Hook. & Grev.) Robins.
Trichostomum brachydontium Bruch
Weissia latiuscula C. Muell.

Grimmiaceae (15)
Grimmia laevigata (Brid.) Brid.
G. pulvinata (Hedw.) Sm.
Leucoperichaetium eremophilum Magill

APPENDIX I. Continued.

Gigaspermaceae (16)
Chamaebryum pottioides Thér. & Dix.
Gigaspermum repens (Hook.) Lindb.

Funariaceae (19)
Funaria bergiana (Hornsch.) Broth.
F. hygrometrica Hedw.
F. micropyxis (C. Muell.) Broth.
F. rhomboidea Shaw
Goniomitrium africanum (C. Muell.) Broth.
Physcomitrium spathulatum (Hornsch.) C. Muell.

Bryaceae (24)
Brachymenium acuminatum Harv.
B. dicranoides (Hornsch.) Jaeg.
Bryum alpinum Huds. ex With.
B. argenteum Hedw.
B. bicolor Dicks.
B. capillare Hedw.
B. cellulare Hook. in Schwaegr.
B. nitens Hook.
B. radiculosum Brid.

Bartramiaceae (37)
Philonotis dregeana (C. Muell.) Jaeg.
P. falcata (Hook.) Mitt.
Ptychomitriopsis sp.
P. africana Dix.—no locality

Erpodiaceae (40)
Erpodium transvaalense Broth. & Wag. in Dix.

Fabroniaceae (70)
Fabronia perciliata C. Muell.

Leskeaceae (71)
Lindbergia sp.

Plagiotheciaceae (76)
Plagiothecium rhynchostegioides C. Muell.

ESPÈCES RARES ET EN VOIE D'EXTINCTION DE LA FLORE DE LA CÔTE D'IVOIRE

LAURENT AKÉ ASSI[1]

On assiste, impuissant, depuis plus de 25 ans, dans la plupart des pays africains sud-sahariens en général et dans les îles adjacentes, à une destruction généralisée par l'homme du couvert végétal, avec une rapidité sans précédent. Ce qui a occasionné une variation notable des climax. Les grands ensembles floristiques, humides, ou xérophiles ont subi des régressions ou des expansions. Les forêts précèdent les peuples; les déserts les suivent. La cause principale de cette situation est l'utilisation irrationnelle de l'espace végétal. En effet, l'équipement des Etats et l'emprise croissante des hommes sur l'espace naturel font peser des menaces grandissantes sur la biocénose.

En Côte d'Ivoire, la mise en valeur industrielle du territoire a eu pour effet, l'exploitation inconsidérée de portions très importantes de la végétation naturelle, entrainant, comme conséquence, la disparition de nombreuses espèces végétales; parmi celles-ci figurent des plantes intéressantes, soit par leur rareté, soit par leur endémisme, soit par leur vertu thérapeutique en médecine de tradition africaine.

Si l'on n'intervient pas assez rapidement pour remédier à cette situation, soixante-six espèces de plantes vasculaires disparaîtront de la flore ivoirienne avant la fin de cette décennie:

1 *Afrormosia elata* Harms (Papilionaceae)
2 *Alafia multiflora* (Stapf) Stapf (Apocynaceae)
3 *Aponogeton vallisnerioides* Baker (Aponogetonaceae)
4 *Aptandra zenkeri* Engl. (Olacaceae)
5 *Argostemma pumilum* Benn. (Rubiaceae)
6 *Aristolochia embergeri* Noz. et Hallé (Aristolochiaceae)
7 *Asplenium brausei* Hieron. (Aspleniaceae)
8 *Begonia rostrata* Welw. ex Hook. f. (Begoniaceae)
9 *Burmannia madagascariensis* Mart. (Burmanniaceae)
10 *Chlamydocardia buettneri* Lindau (Acanthaceae)
11 *Cleidion gabonicum* Baillon (Euphorbiaceae)
12 *Conocarpus erectus* L. (Combretaceae)
13 *Crotalaria doniana* Baker (Papilionaceae)
14 *Diceratostele gabonensis* Summerh. (Orchidaceae)
15 *Dicraeanthus taylori* De Wild. et Guillaumet (Podostemaceae)
16 *Dioscorea quartiniana* A. Rich. (Dioscoreaceae)
17 *Diospyros tricolor* (Schum. et Thonn.) Hiern (Ebenaceae)
18 *Dorstenia embergeri* Mangenot (Moraceae)
19 *Drosera indica* L. (Droseraceae)
20 *Drypetes aframensis* Hutch. (Euphorbiaceae)
21 *Drypetes laciniata* Hutch. (Euphorbiaceae)
22 *Drypetes singroboensis* Aké Assi (Euphorbiaceae)
23 *Eleocharis naumanniana* Boeck. (Cyperaceae)
24 *Epithema tenue* C. B. Clarke (Gesneriaceae)
25 *Fagara mezoneurospinosa* Aké Assi (Rutaceae)
26 *Fagara psammophila* Aké Assi (Rutaceae)
27 *Gerrardanthus paniculatus* (Masters) Cogn. (Cucurbitaceae)
28 *Gymnosiphon longistylus* (Benth.) Hutch. (Burmanniaceae)
29 *Haplormosia monophylla* (Harms) Harms (Papilionaceae)
30 *Heteradelphia paulojaegeria* Heine (Acanthaceae)
31 *Hexalobus salicifolius* Engl. et Diels (Annonaceae)
32 *Hibiscus comoensis* A. Chev. ex Hutch. et Dalz. (Malvaceae)
33 *Hugonia rufipilis* A. Chev. ex Hutch. et Dalz. (Linaceae)
34 *Loesenera kalantha* Harms (Caesalpiniaceae)
35 *Lycopodiella affinis* (Bory) Pic.-Ser. (Lycopodiaceae)
36 *Macrosphyra brachysiphon* Wernham (Rubiaceae)
37 *Maranthes robusta* (Oliver) Prance (Chrysobalanaceae)
38 *Mesanthemum radicans* (Benth.) Koern. (Eriocaulaceae)

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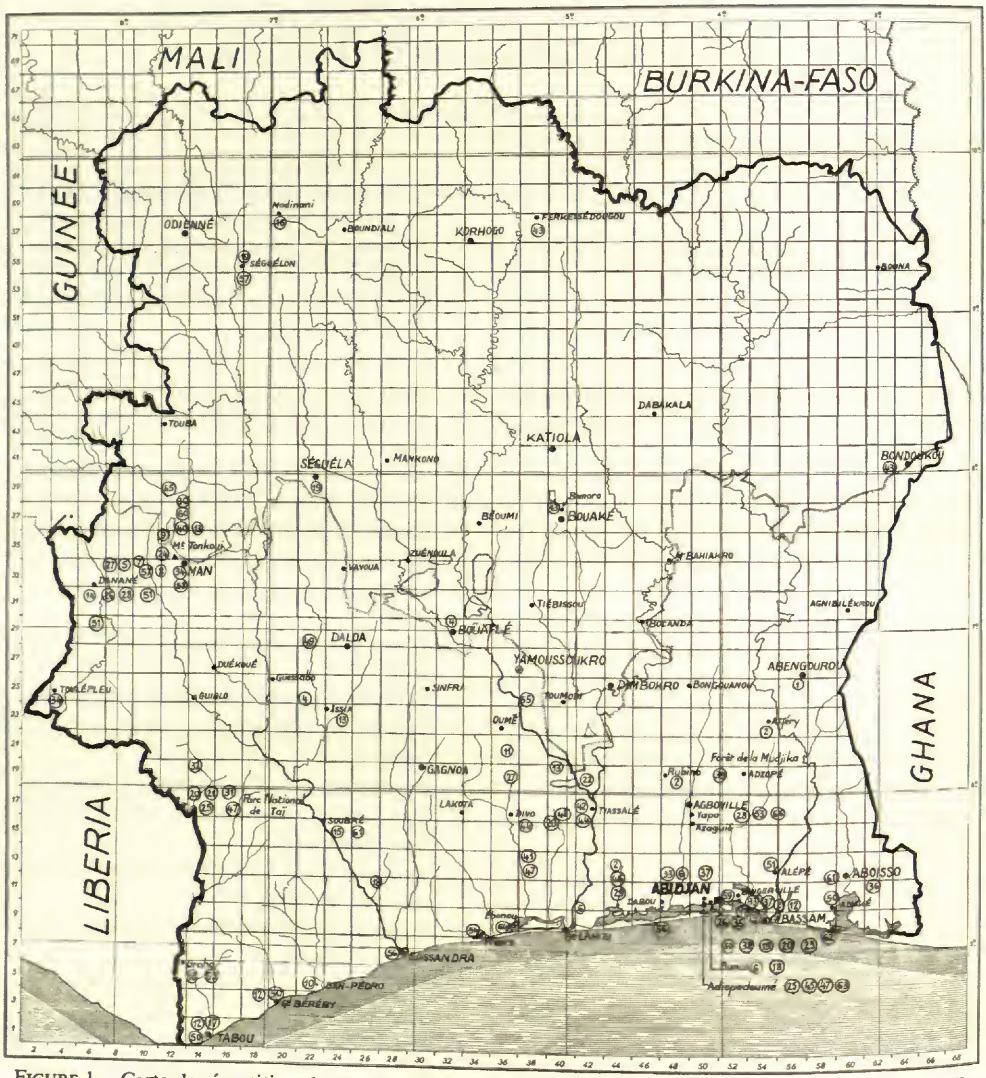

FIGURE 1. Carte de répartition des espèces en voie d'extinction de la flore de la Côte d'Ivoire. Les chiffres sont ceux correspondant à la liste alphabétique des plantes concernées.

39 *Monanthotaxis capea* (E. G. Camus) Verdc. (Annonaceae)
40 *Neoschumannia kamerunensis* Schltr. (Asclepiadaceae)
41 *Nothospondias staudtii* Engl. (Anacardiaceae)
42 *Notobuxus acuminata* (Gilg) Hutch. (Buxaceae)
43 *Pararistolochia goldieana* (Hook. f.) Hutch. et Dalz. (Aristolochiaceae)
44 *Pisonia aculeata* L. (Nyctaginaceae)
45 *Psilotum nudum* L. (Psilotaceae)
46 *Rhaptopetalum beguei* Mangenot (Scytopelaceae)
47 *Rhigiocarya peltata* J. Miège (Menispermaceae)
48 *Rivina humilis* L. (Phytolaccaceae)
49 *Rorippa madagascariensis* (DC.) Hara (Brassicaceae)
50 *Scaevola plumieri* (L.) Vahl (Goodeniaceae)
51 *Schizocolea linderi* (Hutch. et Dalz.) Bremek. (Rubiaceae)
52 *Sciaphila africana* A. Chev. (Triuridaceae)
53 *Sebaea oligantha* (Gilg) Schinz (Gentianaceae)
54 *Sesuvium portulacastrum* (L.) L. (Aizoaceae)
55 *Solanum terminale* subsp. *inconstans* (C. H. Wright) Heine (Solanaceae)

56 *Sophora occidentalis* L. (Papilionaceae)
57 *Streptocarpus nobilis* C. B. Clarke (Gesneriaceae)
58 *Strophanthus barteri* Franch. (Apocynaceae)
59 *Strophanthus thollonii* Franch. (Apocynaceae)
60 *Strychnos chromatoxylon* Leeuwenb. (Loganiaceae)
61 *Synsepalum aubrevillei* (Pellegrin) Aubrév. et Pellegrin (Sapotaceae)
62 *Synsepalum tsounkpe* Aubrév. et Pellegrin
63 *Tarenna hutchinsonii* Bremek. (Rubiaceae)
64 *Teclea carpopunctifera* A. Chev. (Rutaceae)
65 *Vanilla imperialis* Kraenzl. (Orchidaceae)
66 *Voyria primuloides* Baker (Gentianaceae)

Six autres espèces, quantitativement bien représentées dans les différentes formations végétales climaciques du pays, sont menacées de disparition du fait de leur exploitation abusive pour divers usages domestiques traditionnels. Ce sont *Iodes liberica* Stapf (Icacinaceae) et *Momordica angustisepala* Harms (Cucurbitaceae) sont deux lianes, dont les tiges servent à confectionner des éponges; les fragments de tige et les petites racines de *Garcinia afzelii* Engl. et de *Garcinia kola* Heckel (Clusiaceae) sont utilisés comme frotte-dents; deux palmiers lianes, *Eremospatha hookeri* (Mann et Wendl.) Wendl. et *Eremospatha macrocarpa* (Mann et Wendl.) Wendl. (Arecaceae), ont leurs tiges qui sont employées en sparterie et en vannerie.

Le problème de protection de la nature est d'actualité. C'est pourquoi il paraît hautement souhaitable que l'attention de l'opinion internationale soit attirée sur le danger qui menace les espaces naturels des pays en développement, afin que soient envisagées des mesures adéquates pour la sauvegarde de spécimens importants de nos forêts en péril.

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THE WORK OF THE I.U.C.N. CONSERVATION MONITORING CENTRE AT KEW AND THE FORTHCOMING CENTRES OF PLANT DIVERSITY BOOK

S. J. M. Droop[1]

Directly or indirectly, we depend on plants for our existence. The natural communities they form are the basis of the food chains that sustain us; without plant cover, the continents would have been washed into the sea and the atmosphere would still be anoxic.

As the world population exceeds 6 billion, the demands on the earth's living resources increases, but the area available for their production decreases. Only 11% of the earth's land surface (excluding Antarctica) is suitable for agriculture (F.A.O., 1978, quoted in I.U.C.N., 1980); the rest suffers from drought, mineral stress (nutritional deficiencies or toxicities), shallow depth, excess water, or permafrost. Much of it is disappearing under urban development, while in other places huge quantities of soil are being washed away. In an effort to keep pace with the quickly-increasing imbalance between population growth and living resources, huge areas of natural vegetation are being destroyed to make way for agriculture and livestock farming.

As many as 40,000 plant species could disappear before the middle of next century if nothing is done to prevent it (Raven, 1984). Some may have provided new medicines, new petrol substitutes, new foods, or the genetic diversity with which to improve present food crops; there is no knowing just what will be lost.

In the past, conservation aid has worked on the so-called "fire brigade" philosophy, responding only to emergencies, often with inadequate results. As a step toward prevention of the problems rather than just their cure, the International Union for Conservation of Nature and Natural Resources (IUCN) has produced the World Conservation Strategy, which provides a philosophical approach linking conservation with development, and defining conservation as "the management of human use of the biosphere so that it may yield the greatest sustainable benefit to present generations while maintaining its potential to meet the needs and aspirations of future generations." The challenge IUCN addresses daily is how to put these conservation principles into practice and how to translate good ideas into concrete achievement. A fundamental step in that process is the accumulation of relevant information on conservation issues. Politicians and decision makers need to know, for example, which natural forests in their country contain the wild relatives of important food crops, or which parts of coastline are vital breeding grounds for fish and shellfish. There must be a baseline from which decisions are made and priorities assigned.

Many organizations monitor the environment effectively on a national or local scale, but there is also a need for an international approach, a planet-wide view of conservation, which can provide the knowledge to assess priorities among countries or supply rapid answers regarding issues in any part of the world. Such an approach can also help fill the gaps, providing data on those countries where effective conservation organizations are yet to be developed; these, unfortunately, tend to be the places where most species are threatened and where the issues of conservation and development are most pressing. IUCN's Conservation Monitoring Centre (CMC) was set up to provide this information on global conservation and ensure that the facts are correct and in the right place at the right time. The CMC is itself a contribution to a larger exercise, the Global Environmental Monitoring System (GEMS) of the United Nations Environment Program (UNEP).

The primary function of CMC is the collection, analysis, interpretation, and dissemination of data as a basis for conservation. CMC does this by integrating four monitoring activities (major management units) that cover the status of animal species (Species Conservation Monitoring Unit—SCMU), plant species (Threatened Plants Unit—TPU), wildlife trade (Wildlife Trade

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Monitoring Unit—WTMU), and protected areas (Protected Areas Data Unit—PADU). Of these, only TPU is based at Kew; the other units are in Cambridge, England. Data resulting from these activities are currently handled with a Wang VS 80 minicomputer having approximately 750 megabytes of disc storage. Data from the four units are linked by common geographical and taxonomic coding systems. The result is a highly sophisticated data base capable of producing integrated outputs on a wide range of contemporary conservation issues.

The Threatened Plants Unit (TPU)

The small staff of TPU depends for its data on a worldwide network of specialists, many of whom are experienced field botanists with an extensive knowledge of the local flora. The unit operates geographically, dividing the world's areas among its research staff, which permits a productive collaboration between TPU and the local botanists. TPU also coordinates a network of ca. 250 botanical gardens that share a concern for the ex situ conservation of the world's rare plants.

Incoming information is stored in three different ways:

1. *Manual files.* The original information (the bulk consisting of correspondence and unpublished reports) is filed in a manual filing system. From there, information is summarized in the form of text "data sheets" and as summary tabulations.
2. *Data sheets.* These are handled in a word processing system. Text files are flexible and can contain any amount and complexity of information, and so can be used to cope with the inherent variability of biological data. The text can be rapidly updated as new information arrives. These sheets form the basis of the Red Data Books.
3. *Data files.* Computers cannot readily process and extract data from plain text files, so summaries of information are coded into data processing files. This enables information to be selected, sorted, and reproduced rapidly in a variety of output formats appropriate to the situation.

The traditional approach of TPU has been to assemble information on the conservation status of individual species worldwide. Floras, monographs, annotated checklists, and other taxonomic works are screened, and for each country a series of data cards is drawn up, one for each so-called "candidate" species. These are species indicated to be of restricted distribution, which therefore, in the absence of detailed information, show a potential of being threatened. The cards are annotated with the plant name, authority, family, endemism code (single country endemic, regional endemic, etc.), distribution (as indicated in the publication), and any other relevant notes. From this information, lists of candidate endemic and nonendemic species are prepared for each country and these are distributed around the network of contacts as appropriate, to be annotated with the IUCN categories of conservation status used in the Red Data Book series. As each list is returned, the information is transferred to the card index and from there into the data file of the computer. On 18 May 1985, CMC's computer held information on 14,781 threatened plant species worldwide in a total file of 31,477 plants.

As a corollary of this, there is enough information available on some species for a full data sheet to be written. This includes a description of the status, distribution, habitat, and ecology of the plant, along with its biology and potential value, any conservation measures already in force, and any proposed. The data sheet also includes a description of the plant. A selection of 250 data sheets was published in 1978 as *The IUCN Plant Red Data Book,* designed to alert the world to the plight of plants and to give examples of the sorts of plants in danger and the variety of threats they face. It was the first international account of threatened plants and of the need to ensure their conservation, and was successful in bringing attention to the fact that many plants as well as animals are threatened.

Since the publication of *The IUCN Plant Red Data Book,* many countries have prepared Red Data Books listing and describing their own threatened flora. However, most of these are for the developed world. Few are for tropical countries where plant diversity is greatest and where the threats to plants are often most acute. The individual species approach works well for areas, mostly temperate, with well-known floras, but for many tropical countries the state of knowledge of the flora has been too fragmentary even to draw up reasonably accurate lists of endemics. This unfortunately has been as true of Africa as of tropical America or Asia. Even with a list of endemics, the distribution patterns of tropical plants mean that an assessment of the conservation status of a particular species is often impossible. So far it has not proven practicable

to compile lists of threatened plants for most tropical countries. However, the computerization of the African flora would ease our approach considerably by bringing together some of the very diffuse strains of knowledge of African taxonomy from the literature.

The IUCN *Centres of Plant Diversity* Book

While the screening of taxonomic literature and the collection of information on threatened species will continue to be an important part of the work of TPU, a new approach is needed, relevant to the pressing issue of species extinctions in the tropics.

We are increasingly convinced that the way to conserve most plant species is to protect large areas of intact vegetation in plant-rich areas, without necessarily knowing each of the plants included. A defined area on a map has a much greater potential of being conserved than has an individually defined species or family. Legislation based on taxa is not practicable or enforceable, except for some species endangered by the international horticultural trade, for example, and many of these species are easily recognized.

With this in mind, we are preparing a set of accounts of sites rather than individual species. It will contain data sheets on 100–150 botanical sites considered by IUCN to be indicative of those in greatest need of protection and where plant species diversity and/or endemism is particularly high. We believe this approach will complement the earlier, species-based volume best. The Red Data Books are some of IUCN's most prestigious publications, and so it is hoped that this next book in the series will generate enough pressure for action to be taken on a number of the sites included.

The book will include three main types of data sheet: defined botanically rich areas where conservation is a top priority (e.g., Mt. Mulanje, Mt. Kinabalu, Mt. Parnassus); threatened vegetation types in danger of destruction but less well defined geographically (e.g., the lowland rain forests of Kalimantan or Cameroon); and threatened floral elements (e.g., the succulent flora of Somalia), again poorly defined geographically. It is not intended to be the final comprehensive account of all the most important sites in the world that are in danger, but rather an indicative inventory. We are saying that the sites chosen are 150 of those with the best potential for saving plants. Clearly, the closer the list of sites is to the 150 best, the better, and great care is being taken to ensure that the areas included in the book are among those of top priority for conservation.

The selection of sites is crucial. The selection of sites and vegetation types (i.e., "sites units") for inclusion in the book will be based principally on a requirement that each must have one or both of the following characteristics:

1. The site unit is evidently species-rich, even though the total number of species present may not be accurately known.
2. The site unit is known to contain a large number of species endemic to it.

The following characteristics will also be considered in the selection and may provide criteria for more detailed site selection at local level, e.g., within a vegetation type:

a. The site is threatened or under imminent threat of large-scale devastation.

b. The site includes a diverse range of habitat types.

c. The site contains a significant proportion of species adapted to special edaphic conditions (e.g., limestone and ultramaphic floras).

d. The site contains an important gene pool of plants of value to man or plants that are potentially useful.

From the above criteria it is clear that political boundaries have little to do with the selection of sites. Thus, there may be countries with more than one site included, whereas others may not have any sites that qualify. Since we are choosing only 150 or so from the whole world, it is necessary to pick only those sites that are of global botanical importance.

The African Sites Proposed for Inclusion

Of the world's 250,000 or so flowering plants, roughly one quarter occur in Africa and Madagascar. If the same proportion is used for the selection of sites for the book, Africa and Madagascar would contribute 37 areas out of 150—perhaps a few more if the greater extent of floristic knowledge in Africa than in tropical America, for example, is taken into consideration.

The selection of the African sites has been a long and involved process. In a sense it started with the 1966 AETFAT Congress held in Uppsala, Sweden, the proceedings of which were published in 1968 (Hedberg & Hedberg, 1968). At that congress, representatives of many countries presented what they considered to be the most important areas for the conservation of plants within the country. At the end of the congress a list was produced of 37 areas considered to be

of prime botanical importance and in need of priority conservation action. This important work put the need for plant conservation in Africa on a firm scientific footing, but it must be said that it was not in a form which aid agencies and other organizations could readily use and so has remained more or less unimplemented since its inception. Now it is hoped that, by collaboration between AETFAT and IUCN, the most important sites in Africa can be highlighted and publicized in a form on which decision makers can act. IUCN, as the union of the conservation organizations of the world, is in a good position to promote the implementation of the book through the activities of the members, which include governments, government agencies, and nongovernmental organizations. The emerging list of the most important sites is, to an extent, different from the original list, partly because the conservation status of some sites has changed, and some areas of botanical importance not appreciated then have been discovered. For example, it is only within the last five years that botanical exploration of the Imatong Mountains in Sudan has revealed that they harbor almost half of the country's flora.

Another major influence in the selection of the African sites has been the 20–30 botanical sites chosen worldwide by IUCN for conservation action under the IUCN/World Wildlife Fund (WWF) Plant Program. The Centres of Plant Diversity book will build on these and provide the blueprint for a much larger program of conservation action and aid, not only by WWF but by IUCN's other conservation partners as well. For Africa, those with projects funded or in the project development phase include Taï National Park (Ivory Coast), Sapo National Park (Liberia), lowland Cameroon rain forests, Tanzanian montane forests (especially Usambaras and Uzungwas), and Aïr and Ténéré (Niger).

As Raven (pers. comm.) has clearly pointed out, the areas in Africa and adjacent islands of greatest importance are South Africa and Madagascar, with roughly 23,000 and 8,200 species, respectively. The list of proposed sites here presented clearly does not take full account of these important areas. For Madagascar, this is because we have far too little information with which to write data sheets; for South Africa, the reasons are less clear, but certainly in part due to the problem of coordinating conservation activity. Nevertheless, these are the countries where action must be taken quickly to prevent massive numbers of species extinction, and efforts made to correct this imbalance.

Conclusion

This paper, then, is a plea to botanists to share their expertise. Firstly, we need to know that the sites chosen are those which, if protected, will save the greatest numbers of species. Secondly, we need advice on whether to write data sheets on the undefined sites as they are, or whether important sites should be specified within each broad area or vegetation type. If the latter, then please help!

Any suggestions for additions, deletions or changes to the list of sites will be gratefully received, as will any help that can be given to write the data sheets. Many of them can be written from library research, but for up-to-date news and insight, it is best that each draft is reviewed by an expert. In many cases, time permitting, botanists may volunteer to write the data sheets themselves, and this help will be most welcome.

A brochure outlining the *Centres of Plant Diversity* book can be obtained from the IUCN Threatened Plants Unit, 53 The Green, Kew, Richmond, Surrey TW9 3AA, England.

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Appendix I.

Candidate list of sites for continental Africa and the islands of the western Indian Ocean.

North Africa
- A part of the High Atlas (Morocco)
- Jabal al Akhdar (Libya)

Tropical and South Africa
- Gebel Elba (Egypt/Sudan)
- A part of the Aïr/Ténéré area (Niger)
- Loma Mountain forests (Sierra Leone)
- Gola high forest (Sierra Leone)
- Mt. Nimba (Liberia/Guinea/Ivory Coast)
- High plateau of Fouta Djallon (Guinea)
- Taï Forest (Ivory Coast)
- A part of southeast Nigeria
- Mt. Cameroon (Cameroon)
- The lowland rain forest of Cameroon

APPENDIX I. Continued.

A part of Gabon
A part of the Haute Katanga (Zaïre)
Low altitude coastal forests (Kenya/Tanzania)
Montane forests of Tanzania
  Usambara Mountains
  Uzungwa Mountains
Mt. Mulanje (Malawi)
A part of Mbala District (Zambia)
Huilla Plateau (Angola)
The flora of the Kalahari Sands (Zambia, Zimbabwe, Botswana, and South Africa)
The serpentine flora of the Great Dyke (Zimbabwe)
The succulent flora of Somalia
Imatong Mountains (Sudan)
Forests of southwest Ethiopia
Simien Mountains (Ethiopia)
A part of the Cape Floristic Region (South Africa)
Western Indian Ocean
  One or more parts of Madagascar
    Eastern moist forests
    Western deciduous forests
    Southern spiny thicket
  Reunion Island
  A part of Socotra Island

CONSERVATION STATUS OF THE KAKAMEGA FOREST IN KENYA: THE EASTERNMOST RELIC OF THE EQUATORIAL RAIN FORESTS OF AFRICA

J. O. KOKWARO[1]

ABSTRACT

The Kakamega Forest in Kenya is the easternmost relic of the equatorial forests that stretched across the Zaire basin from the Atlantic coast. It is related to the equatorial rain forests of West Africa, Zaire, and Uganda but has a cooler and less humid climate. The gazetted forest reserve consists of approximately 23,777 hectares of the main forest block. Other closely associated smaller forests are Kisere Forest (484 ha.), Malaba Forest (718 ha.), and Bunyala Forest (825 ha.). A considerable reduction in forest area has occurred during the past two or three decades and, in the case of Bunyala Forest, there is hardly any natural forest left. The Forest is continually being overused, with resulting serious degradation and deforestation. The increase in population in western Kenya has created a strong demand for more land for food production. To maximize conservation with tolerable levels of human exploitation, a policy of development without destruction is recommended for managing the remaining forests. Checklists of woody and herbaceous species, as well their vernacular names, are provided in Appendices.

RÉSUMÉ

La forêt Kakamega au Kenya est le reste le plus oriental des forêts équatoriales qui s'étendaient de la côte atlantique à travers le bassin du fleuve Zaïre. Elle a des affinités avec les forêts pluviales équatoriales de l'Afrique occidentale, du Zaïre et de l'Uganda, mais son climat est plus frais et moins humide. La réserve forestière officiellement publiée comprend à peu près 23,777 ha du bloc forestier principal. D'autres forêts plus petites et étroitement associées sont Kisere (484 ha.), Malaba (718 ha.), et Bunyala (825 ha.). Pendant les 20 ou 30 années dernières on a remarqué une diminution considérable de la superficie des forêts, et il ne reste guère plus de végétation naturelle dans la forêt Bunyala. L'utilisation continuelle et excessive de la forêt Kakamega a des résultats très graves de dégradation et de déforestation. L'accroissement démographique au Kenya occidental a créé une forte demande de terrains pour la production alimentaire. Pour porter au maximum la conservation avec des niveaux tolérables d'exploitation humaine, on recommande ici une politique de développement sans destruction dans l'administration des forêts restantes. L'auteur donne des listes des espèces ligneuses et herbacées, de même que leur noms vernaculaires, dans les annexes.

Tropical rain forest is evergreen humid forest receiving an annual rainfall of at least 1,600 mm/yr. In zones with very heavy rainfall the tree crowns are normally at a height of 30–40 m and the tallest trees are 70 m or more. The tropical rain forests are located primarily along the Equator and between the two tropics in Africa, Asia, and Latin America. The early European explorers referred to these forests as "green hells" or "impenetrable jungles." Whereas there may be 10 different indigenous tree species per hectare in European forests, in a tropical rain forest there are often 100–150 different tree species in the same area. Species diversity in different parts of a forest is considerable. In the African rain forests, 40% of the mammals live in the trees. Certain kinds of amphibians and reptiles live only in trees. Roughly two-thirds of the mammals are nocturnal and escape observation almost completely, since they pass the day hidden in the hollow of a tree or high above ground in the tree canopy. Tropical forests are a valuable reservoir of genetic material so long as they remain intact.

Kakamega Forest (Fig. 1) is the easternmost relic of the equatorial forests that stretch across the Zaire basin. It therefore contains variants of species that, being on the extreme fringe of the range, are adapted to environments slightly different from the stocks in the center of these forests. (Checklists of woody and herbaceous species recorded in the Kakamega Forest, as well as their vernacular names, are provided in the Appendices.) Although originally stated to cover some 230 km^2, this forest now covers roughly a little over 100 km^2 and is being steadily destroyed by timber cutters, charcoal burners, firewood collectors, and development planners who wish to replace the primary forest remnants with fast-growing exotic tree plantations, cash crops such as tea or sugar cane, or settle more families in

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FIGURE 1. The gazetted boundaries of tropical rain forests of Kakamega District and their allies, the Nandi Forests.

the land. Just as in the other parts of tropical Africa, deforestation in Kakamega Forest is believed to have been especially marked during the last 20 years, primarily due to the expanding need for land by the largely agricultural population surrounding the forest. Discussions with the elders in the province reveal that before World War II, Kakamega Forest and the adjacent forests covered three to four times their present areas. The bioclimatic changes recorded in the present generation suggest that two centuries ago there could have been twice as much again of the amount that was there in the 1940s. At the present rate of deforestation, Kakamega Forest will be entirely eliminated shortly after the turn of the century. During 1966, in a sampling survey of the indigenous forest of Kakamega, the Inventory Section of the Kenya Forest Department recorded the total area as 25,600 ha.; merchantable strata 16,700 ha.; commercial species

667,800 m^3 (33 cm dbh or more); and noncommercial species 2,482,300 m^3 (33 cm dbh or more).

Kakamega is the only tropical rain forest of the Guineo–Congolean type found in Kenya. It is located in western Kenya to the west and directly below the Nandi Escarpment between latitudes 0°10′ and 0°21′N and longitudes 34°47′ and 34°58′E. Its altitude above sea level varies between 1,520 m and 1,680 m, and the gazetted forest reserves consist of approximately 23,777 ha. Closely associated with it both geographically and biologically are three smaller forest blocks: Kisere Forest, located some 6 km to the north, covers some 484 ha.; Malaba (Malava or Mlaba) Forest, located some 12 km to the north along the Bungoma road, has an area of some 718 ha.; and Bunyala Forest, some 14 km to the northwest, has an area of about 825 ha. Many changes have taken place in the past two decades, and in the case of Bunyala Forest there is hardly a natural forest cover of more than 10 ha. today. Two major rivers pass through the forest, each with several tributaries, particularly in the eastern blocks of the forest. In the northern section of the forest is the Isiukhu River, which rises in the North Nandi Forest and the Nandi Escarpment. The southern section of the forest is dissected by the Yala River, together with its many tributaries with sources mainly in the Tinderet Forest and South Nandi Forest.

One of the major problems resulting from the rapid destruction of the natural communities of the forest and the depletion of species is that future generations will undoubtedly be deprived of the natural resources and essential water supplies. Also, habitat for several bird and primate species will be lost. Over four decades ago, Kakamega Forest consisted of fairly thick continuous tropical rain forest with interspersed grassy glades where the underlying rock formations are close to the surface, making the soil too shallow to support forest trees. Similar tropical rain forest species and forest patches containing *Antiaris toxicaria, Milicia excelsa, Ficus storthophylla, Funtumia latifolia,* and other giant trees still grow wild in places as far as Yala and Butere some 30 km west of Kakamega Forest. Such forest patches are also found near Bukura toward Butere, and personal communication from some old men in western Kenya reveals that most areas in the present Western Province, parts of Gem, and Ugenya in Siaya District had thick forests and woodlands some 70 years ago. The forest is continuous with the South Nandi Forest on the southeast, but is bordered to the east, north, west, and southwest by wet *Combretum* woodland. It is believed that the *Combretum* woodland is a secondary plant community that appears in areas that have been gradually cleared of forest and turned into farmland or pasture. During the last 30 years, sawmilling, followed by complete clearance for agriculture, has greatly reduced the area covered by indigenous forest, and today large areas of former forest are occupied by either farms primarily for maize or by exotic timber plantations. The Forest Department has also had a policy of licencing lumber companies to completely clear indigenous forest areas and allowing the local people to plant maize on the land for 4–7 years. In the last two years the Department interplants exotic tree seedlings with maize before finally taking back the land as a new plantation. The Department is also replanting fast-growing indigenous trees such as *Maesopsis eminii.*

Historical Background

When the British Government assumed direct control of Kenya in 1895, the first major task undertaken was the construction of the railway from Mombasa to Port Florence (Kisumu) on the shores of Lake Victoria. From the forestry point of view, the need to ensure large supplies of fuel for the wood-burning locomotives led to the establishment of the first up-country forest reservation and to the first plantations of eucalypts for fuel. During the time of the first European settlement in Kenya, there was substantially more closed forest than there is today. The early explorers found the forests in widely scattered blocks, and these included the Kakamega–Nandi–Tinderet system or block. In the distant past there was no doubt much more closed forest than was found by the early European settlers. Parts had already been cleared by the advance of African shifting cultivators and by repeated firing of grasslands by pastoral tribes. Kakamega Forest and any other scattered blocks of forest still remaining in the country had survived in special circumstances of noninflammability due to their wetness or because they were montane, cold, or inaccessible.

Although the Lake Victoria basin or Victoria Nyanza basin forest system is only moderately wet (rainfall 1,200–2,600 mm per annum), it is biologically similar to the equatorial rain forests of West Africa, Zaire, and Uganda but rather

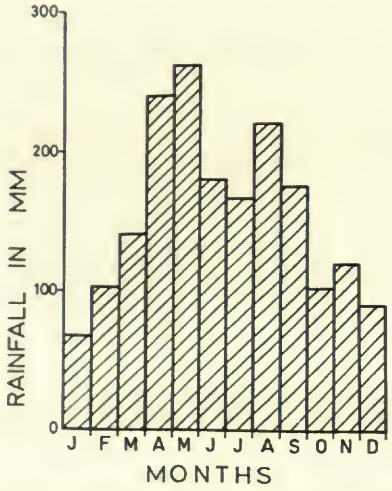

FIGURE 2. Mean monthly rainfall calculated for 60 years of data from the Western Agricultural Research Station in Kakamega.

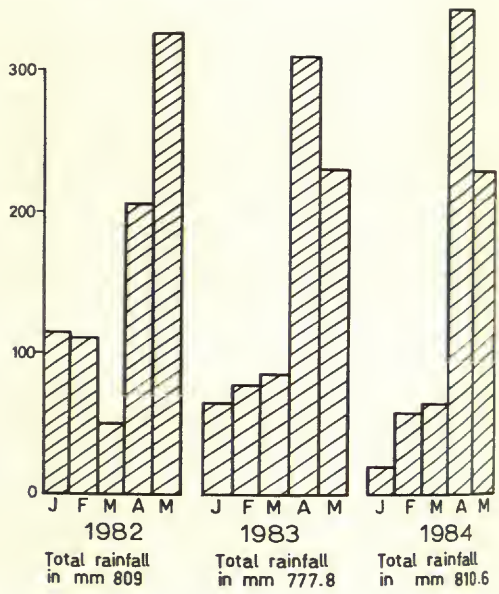

FIGURE 3. Monthly rainfall at Western Agricultural Research Station in Kakamega for January through May of 1982, 1983, and 1984.

cooler and less humid. Kakamega Forest is the easternmost block of the true tropical equatorial rain forest in Africa. From the forester's point of view, it has been regarded as difficult to manage, since it yields a number of good quality hardwood timbers but the total quantities are small and most species take too long to mature. There seems to be a slight change in the present amount of rainfall at the Kakamega Forest. Zimmerman (1972) recorded an average precipitation at the Forest Station for a period of three years (1963–1965) as 2,210 mm but adds that during 1963 almost 3,600 mm of rain was recorded. There is an obvious correlation between the decline in the amount of rainfall at the Kakamega Forest now with the deforestation trend in the area. Most recent researchers at the forest have categorized it as a semitropical rain forest with precipitation between 1,250 and 2,000 mm, but we still maintain that Kakamega Forest is a tropical rain forest that lies in a belt of heavy thunderstorm activity comparable to some forests of Uganda. It is believed that the forest contained elephants (*Loxodonta africana*), which were exterminated about 1912, and the Cape buffalo (*Syncerus caffer*), exterminated probably a few years later. It is believed that the Uganda kob (*Adenota kob*) was present in the forest glades and also that the Defassa waterbuck (*Kobus defassa*) were common. Kob are no longer present and the waterbuck is rare. Deforestation and degradation activities in the Kakamega Forest area has changed the climate, the vegetation, the flora, the fauna, and even the species composition to such an extent that most of the early descriptions of the forest no longer apply. The valuable timber tree only known in Kenya from that area, *Gedu Nohor* or *Mukusu* (*Entandrophragma angolense*), now only occurs in the southern block of the Yala River complex where a few trees have been located. Many other plant and animal species once common in the forest are also now reduced in numbers or nearly lost.

CLIMATE

RAINFALL

Kakamega Forest is classified as tropical forest with an average annual rainfall of about 2,000 mm, most of which falls from March to August. The Western Agricultural Research Station (W.A.R.S.) in Kakamega town has operated a weather station continuously since 1923. In the period 1923–1983, the mean annual rainfall was 1,956 mm. The distribution of the rainfall in different months of the years is shown in Figure 2. The long rains in this area are normally within the first six months of the year. Daily rainfall records at the W.A.R.S. from 1 March through 31 May 1984 were obtained and plotted as histograms (Fig. 3). The actual rainfall recorded varied over the three months. March 1984 was a

TABLE 1. Summarized data on minimum and maximum (shade) temperatures in °C recorded at W.A.R.S. for March, April, and May 1984.

	Lowest Minimum	Mean Minimum	Mean Maximum	Highest Maximum	Mean Difference	Number of Observations
March	5.6	14.8	31.1	33.6	16.3	22
April	9.0	15.2	27.1	29.0	11.9	25
May	9.3	15.0	26.4	28.0	11.4	22

comparatively dry month with only 63.5 mm, compared to 344.8 mm and 227.7 mm for April and May.

Records for wind direction are not available.

DIURNAL PATTERNS OF TEMPERATURE AND HUMIDITY

Hygrothermograph records are also maintained at the W.A.R.S. The recorder is lodged in a Stevenson's screen about 1 m above ground level. The traces show the diurnal fluctuation in temperature and humidity at different seasons.

In March through May 1984, temperatures were highest between 12:00 P.M. and 6:00 P.M. Humidity showed the expected inverse relationship to temperature with maxima at 5:00–6:00 A.M., when dewfall occurred. If the rains came in the daytime, the temperature fell abruptly and the humidity rose. Afterwards, the temperature rapidly recovered but the humidity tended to stay high. The humidity rose above saturation every night and heavy dews fell. Diurnal changes in temperature (Table 1) are greater than the seasonal changes. For example, the daily difference between maximum and minimum temperatures for March, April, and May 1984 were 28°, 20°, and 18.2°C as compared to the mean differences in values for the three months of 16.3°, 11.9°, and 11.4°C, respectively.

NATURAL FOREST DEPLETION

It is estimated by KREMU (Doute et al., 1981; Ochanda et al., 1981) that between 1972 and 1976 Kakamega Forest lost 1,180 ha. (8%), and 780 ha. (6%) between 1976 and 1980 (Tables 2, 3). Cleared natural forest areas are often replaced by agriculture or softwood monocultures (Table 4; Figs. 4–6). The depletion rate of area under natural forest cover in Kakamega Forest has a recorded loss of 245 ha. per annum.

CURRENT PROBLEMS AFFECTING NATURAL FOREST

ILLEGAL REMOVAL OF TIMBER

The Forest Department normally licences commercial timber companies to cut mature indigenous forest trees for timber processing. But whereas the licenced timbermen work during the day, the illegal timber cutters come late in the evening, at night, or during holidays to remove rather young but valuable trees from the same area where the legal logging is occurring. Forest trees are illegally removed by the public for use as timber, building poles, charcoal burning, tool handles, etc. This is a type of timber "poaching" and it occurs in every part of the natural forest. Sometimes the tree is cut and left to be collected later or is abandoned whenever a forestry land-

TABLE 2. Depletion rate and trend in the natural forest cover in Kakamega, Bunyala, Kisere, and Malaba forests. Gazetted forest areas includes nonforested areas.

Forest	Gazetted Forest Area (ha.)	Changes in Stocked Forest Area (ha.)				Annual Rates of Changes (ha.)
		1959–1967	1972	1976	1980	
Kakamega	23,777	14,268	14,268	13,088	12,308	245
Bunyala	825	825	0	0	0	0
Kisere	484	472	472	472	472	0
Malaba	718	0	0	205	180	0

TABLE 3. Amount of natural forest cover lost between 1959 and 1980 (in hectares).

Forest	1959–1972		1972–1976		1976–1980		Period of Change (years)
	Amount	% Loss	Amount	% Loss	Amount	% Loss	
Kakamega	0	0	1,180	8	780	6	8
Bunyala	0	0	825	100	0	0	9

rover is heard. Such cut trees can be found in parts of the natural forest apparently forgotten or no longer wanted. Illegal logging is responsible for much of the deforestation of the Kakamega forest.

VANDALISM TO TREES

Vandalism of trees by herd boys is discussed later. Other damage is done by people seeking the bark of certain trees for herbal remedies. The forest could tolerate this kind of human use since the amount of material removed is minimal, but quite often it is the same trees that are used repeatedly until they have been completely ringbarked and die. Some of the largest *Olea welwitschii* specimens have suffered this fate, as well as the heavily used *Warburgia salutaris*.

FUELWOOD COLLECTION

Removal of dead wood for firewood is permitted without special license in the forest outside the nature reserve. The women who collect firewood are usually careful to remove only dead wood. In 1963, Zimmerman found no evidence for the shortage of breeding sites for barbets and woodpeckers despite removal of dead wood, but the situation is now different. With the human population increase that has occurred in the vicinity of the forest over the past 20 years, the effect of human removal of firewood is increasing. The forest probably is able to withstand the pressure now exerted on it, but with the continuing increase in population in the surrounding area, the demand for firewood will increase, whereas the supply from the indigenous forest will not. The problem begs immediate attention.

Apart from the potential overuse of this forest resource, the collection of firewood has some immediate consequences, namely the disturbance that results from the collection process itself. Sometimes many understory plants are smashed or cut in the effort to expose and remove the dead wood. Also, the sound of pangas chopping for several hours a day makes study of wildlife difficult for researchers or tourists.

Charcoal production within and around Kakamega Forest has been and is still a lucrative business. Indigenous trees usually produce the best quality charcoal, hence the high demand for them in charcoal production. Charcoal is a major source of energy in both urban and rural Kenya. Eucalypts and other soft-wood species forming the major part of plantations make poor quality charcoal. There is therefore a heavy demand for the local hardwood species for charcoal production.

TABLE 4. Proportion of plantations to indigenous forest cover in 1980.

Forest	Area Under Plantations (ha.)	Area Under Indigenous Forest (ha.)	Total Area (ha.)
Kakamega	1,690	12,308	13,998
Bunyala	105	0	105
Kisere	0	472	472
Malaba	38	180	218

DESTRUCTION OF SAPLINGS

Saplings are routinely cut by the Forest Department to provide struts that hold up the grass shading the seedlings in the nursery. These saplings are taken from the nature reserve, and it is not illegal for the Forest Department to remove them. However, many are taken from the belt of forest behind the offices at the forest station and are cut in such a way as to leave large swaths of clear-felled undergrowth. (Both *Brillantaisia* and *Dracaena* are cut and used as well.) Since *Brillantaisia*, a light-requiring species characteristic of secondary growth, tends to grow in areas where the canopy is incomplete, clear-felling of the undergrowth often exposes the ground to direct sunlight.

This kind of harvesting has three consequences: (a) it destroys a suitable microhabitat for seedling growth because of the removal of

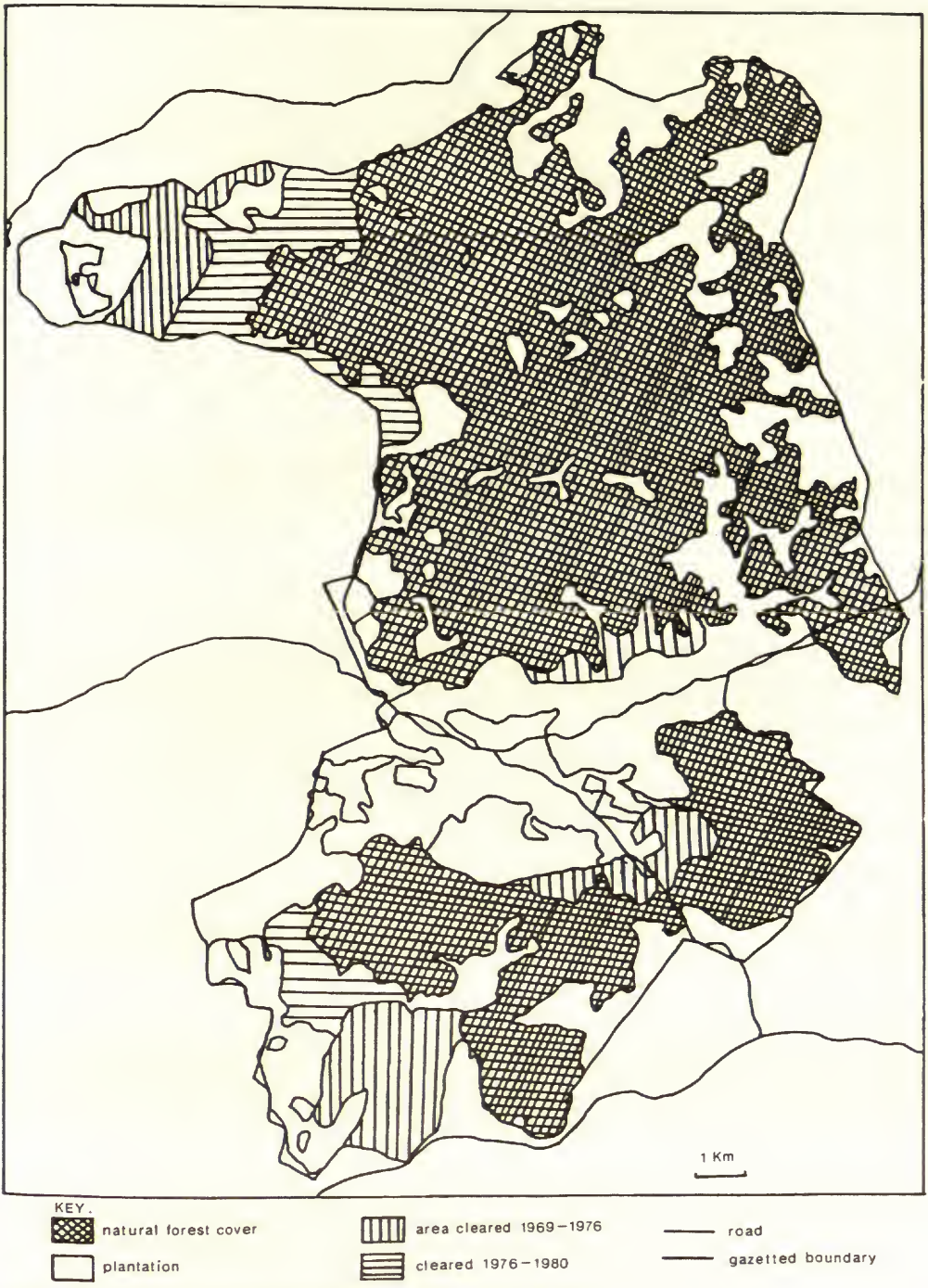

FIGURE 4. Deforestation trends in the Kakamega Forest, 1969–1980.

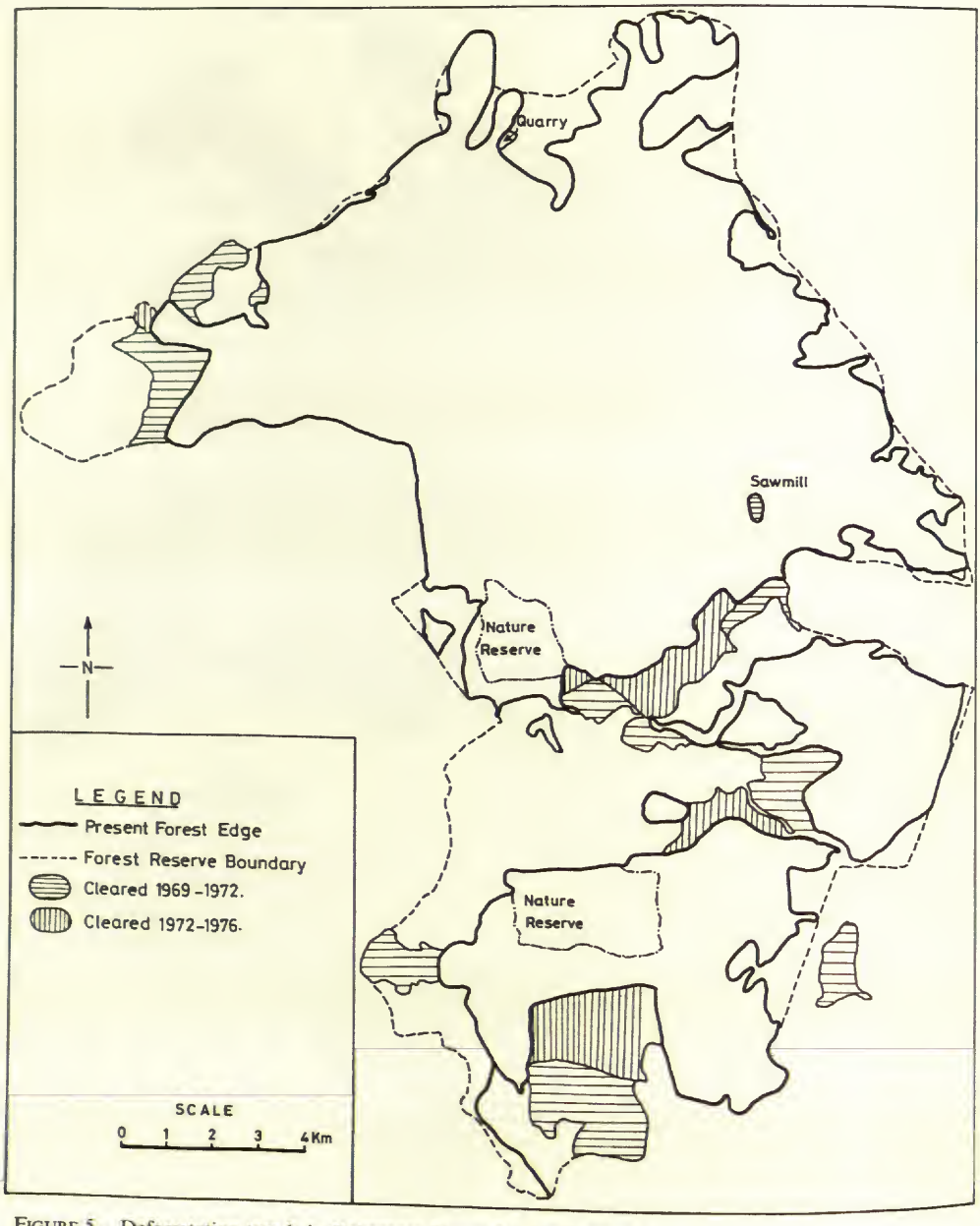

FIGURE 5. Deforestation trends in Kakamega Forest for recent years.

protection from the elements and hence impedes regeneration; (b) it destroys large patches of suitable habitat for understory birds and insects; and (c) it is extremely unsightly. This patch of forest, even though it is not part of the Nature Reserve, has easy access and consequently attracts a disproportionate number of tourists. The occurrence of 400^2 m of felled undergrowth 50 m into the forest on the main trail to Mama Mutere, the oldest tree in the forest and the Nature Reserve, gives a very poor impression of forest conservation to visitors. Saplings are also cut to make fences. It is estimated that 4,500 saplings were used to construct the canteen fence, and in June

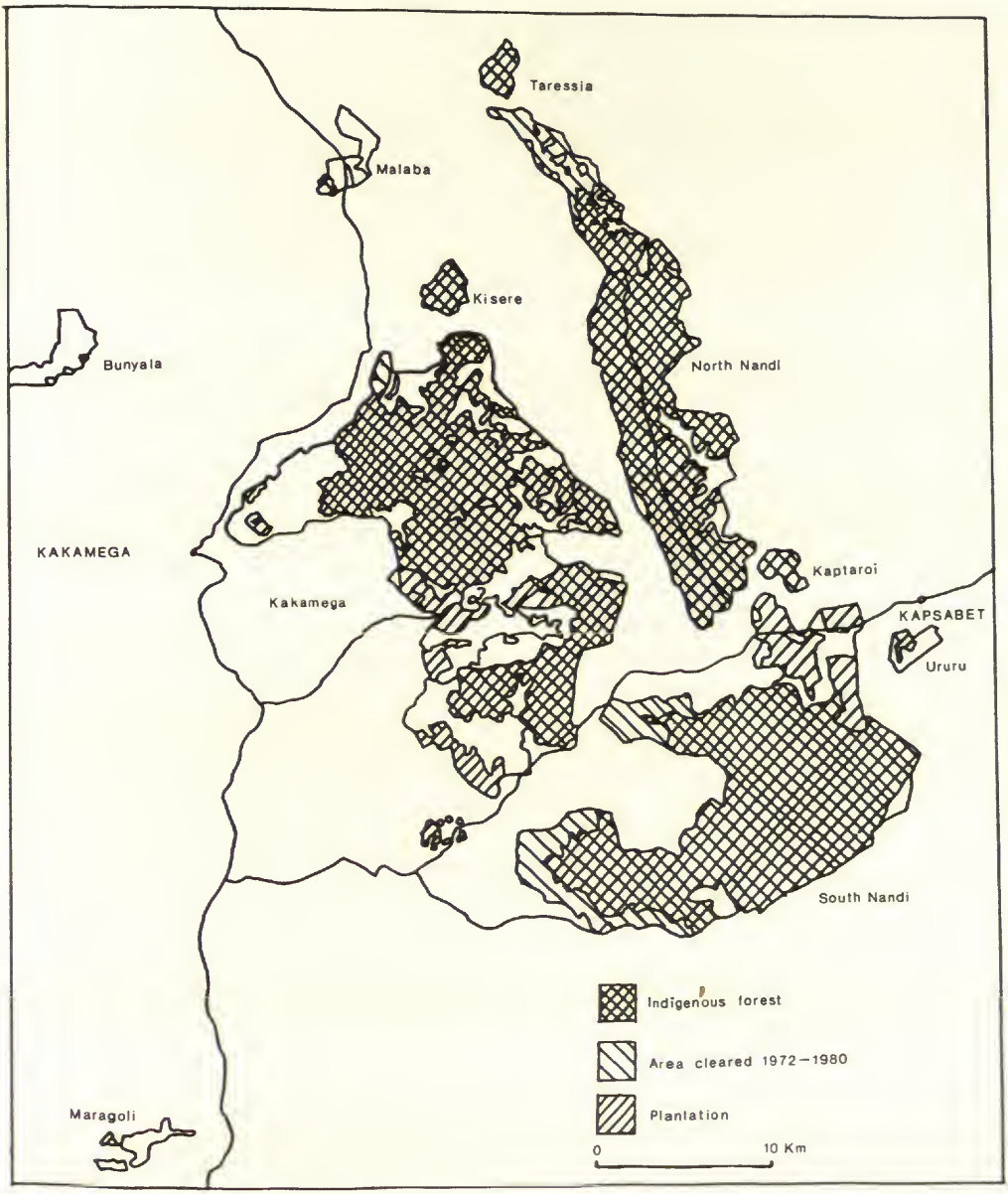

FIGURE 6. The status of the tropical rain forests of Kakamega District and the Nandi Forests by 1980.

1982 another 1,000 lay wasted on the ground nearby. The average diameter of these young trees was about 4 cm.

DESTRUCTION CAUSED BY CATTLE GRAZING

The Forest Department issues grazing permits at minimal cost for any cattle grazing on forest land. Certain grassy areas are specified for grazing, none within the confines of a nature reserve. Nevertheless, nearly every day there are as many as 100 cattle grazing in the forest station nature reserve. This is, of course, strictly illegal, and yet it occurs a mere 600 meters from the forester's office.

Cattle grazing causes damage in two ways. First,

the cattle must reach the grassland by traveling through the forest. In so doing, they trample ever wider paths which become channels of deep, stinking mud in which no plants can grow. When one path has been thus ruined, the same process begins on a new one. The undergrowth is destroyed in such areas and regeneration stops. The paths are impassable through the entire wet season and are dry, rock hard, and bare during the dry season. For a good part of the year then, large parts of the forest become inaccessible to forest guards, researchers, and tourists. Further damage to forest trees is perpetrated by bored herd boys who simply vandalize trees, cutting large slashes in them or cutting them down entirely for no obvious purpose. Second, grazing sometimes leads to destruction in the grassland. During the dry season, the grass is burned in order to improve grazing conditions. The fires are usually abandoned once started and burn unsupervised until they may be noticed by forest guards. At least four burnings have occurred in the nature reserve grassland over the past three years; fortunately, none spread to the surrounding trees.

POACHING OF FOREST GAME

It is hard to assess the extent of poaching of forest game without a directed effort. Traps and snares may be set quietly and are usually placed well off paths. Evidence for the occurrence of poaching is of two kinds: 1) I have seen several times parties of men leading dogs with bells on their collars. In one case, the duiker pursued by such a group was seen running out of the forest into nearby scrub. 2) I have found many traps for guinea fowl (*Guttera edouardi*) in the undergrowth. These are usually nooses placed on a path through thick vegetation or near some maize kernels. On several occasions live birds have been found snared and were released by conservationists. In 1972, when I began my study of the forest, guinea fowl were frequently seen or heard in some parts of the forest. There is no sign of their continued presence 15 years later.

Suggested Solutions to the Problems

To control timber poaching, more effective patrolling is necessary, especially within the proposed National Park (Fig. 7). Constant surveillance is not required, but regular spot checks on a daily basis at a different time each day would help immensely. Again a bonus system could be instituted. But where would people get their wood? Either they must buy it or grow their own. The Forest Department is already active in encouraging people to plant trees through an agroforestry system. The cooperation of local officials must be sought for informing people what the long-term effects of overuse of the forest will have. It is not enough to simply cite the law; the reason behind it must be explained.

Vandalism caused by herd boys would be stopped if cattle were prevented from grazing in the forest. The damage to trees by those seeking medicinal barks is a very local problem, involving only a few people. It would be most effective if these people, whose identities are widely known in the local community, were approached personally and in a friendly way and asked to cut bark from several different trees rather than ring-barking a few favorites. There are plenty of *Olea, Trichilia,* etc. to lend a bit of bark for traditional medicine, as long as it is harvested sensibly. Of course the reasons for changing habits, as well as the benefits of conservation of the forest to the Forest Department, researchers, tourists, and local people, must also be explained. The Forest Department should also raise seedlings of medicinal plant species and distribute them to the local people, particularly the herbalists, to plant.

While the current level of exploitation of dead wood is acceptable, I recommend that (1) people be encouraged to plant their own trees (especially *Eucalyptus*); (2) the Forest Department sell more firewood directly to the local people at reduced rates, since transportation is not required; (3) people be encouraged to scavenge in areas of recently felled plantations where many branches are freely available; and (4) collection of dead wood be carried out with care so as to minimize disturbance to living plants and animals, perhaps under the occasional supervision of a forest guard, and the Forest Department raise seedlings of both exotic and indigenous tree species which could be sold at cheap rates to the local farmers. Farmers should be encouraged to practice an agroforestry system of farming.

A short-term solution to the problem of excessive sapling cutting is: a) the reuse of any poles sturdy enough to withstand another year, and b) more judicious harvesting of poles, such that (i) young hardwoods are passed over in favor of perennial shrubs like *Brillantaisia,* and (ii) no large swaths of undergrowth are cleared. I was told by nursery workers that poles are usually discarded after one year but that most are carried off by the workers for their own use, which il-

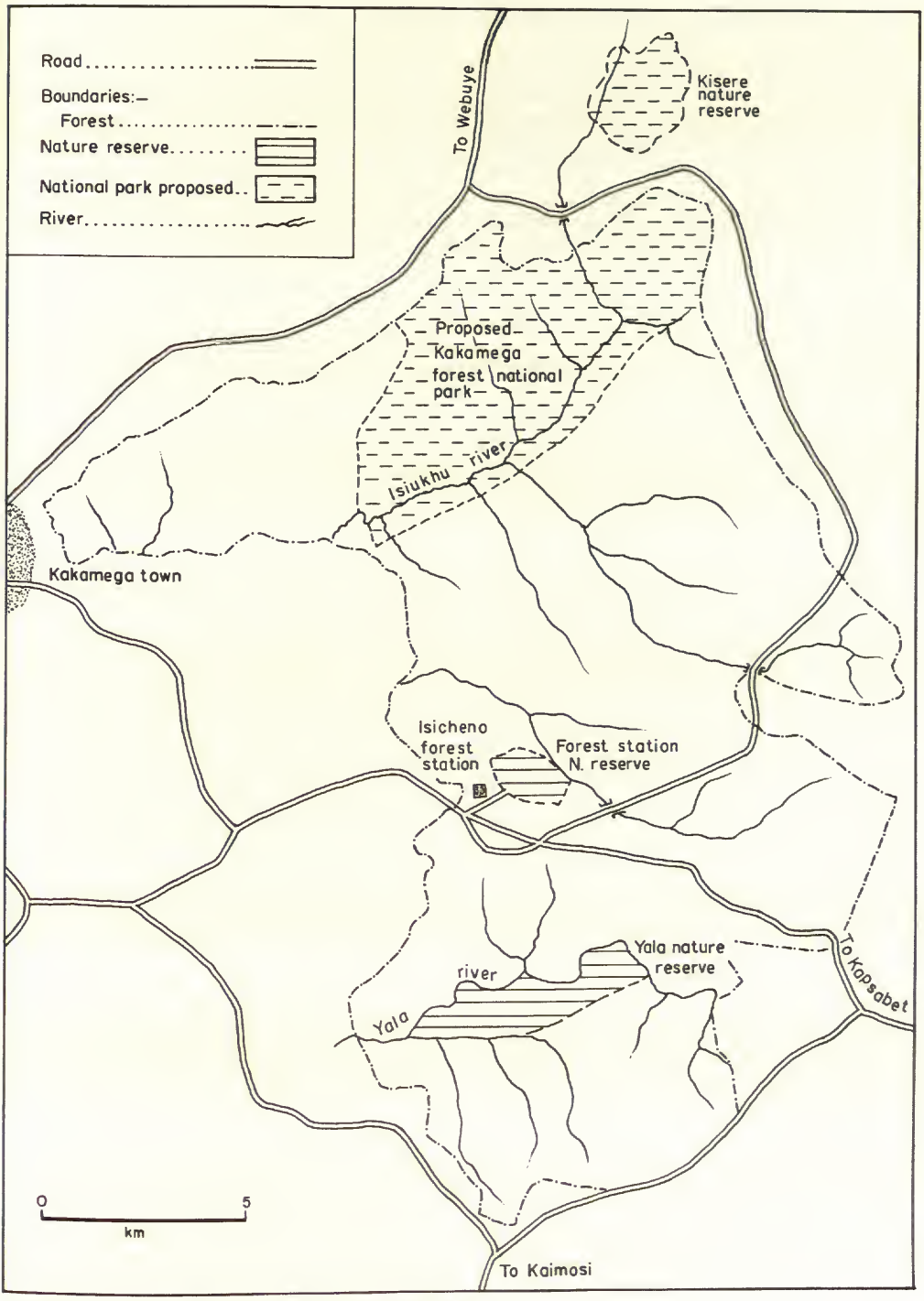

FIGURE 7. Proposed Kakamega Forest National Park.

lustrates their continued value. I also suggest that the Forest Department plant dracaena or bamboo for the express purpose of supporting nursery shades. The forest surrounding the large nursery cannot support the sort of cutting required for shades. Bamboo has the advantage of growing fast and producing straight poles that can be used for several years. After planting, the poles should be stored in a dry place and perhaps treated with wood preservative. As for fencing, I suggest that the Forest Department plant hedges rather than build large wooden fences. If wooden fencing is absolutely required, it should make more modest use of timber.

Vandalism by herd boys would be stopped if cattle were prevented from grazing in the forest. Grazing in the nature reserve glade could be stopped easily if, for example, a forest guard made one daily trip from the forester's office to the glade. Occasionally cattle have been arrested and their owners fined Kshs. 50 per head. For about a week after such raids, cattle did not graze in the nature reserve, but when the forest guards have not continued patrolling the Nature Reserve, the herd boys soon reverted to old habits. Continued surveillance is absolutely necessary. If the Forest Department continues to allow cattle grazing on forest land, it should be confined to glades selected for their accessibility. Access should be limited to a carefully prescribed route, preferably not through forested land. The location of access routes and grazing land must be clearly explained to cattle owners and herd boys when licenses are issued. Pastures should be checked at regular intervals. The Forest Department has in fact adopted such a plan. The pastures where grazing is permitted are not part of the nature reserve, and an access route via Kisaina has been defined. However, these pastures and this route are less convenient to some cattle herders who persist in using the nature reserve illegally. These people do have an alternative, and it should be up to the Forest Department to see that they use it or withdraw the licences.

I have been told repeatedly that there are not enough forest guards to carry out all the patrolling necessary, and this is probably true. There is no patrol on Saturday afternoons, Sundays, or public holidays. Furthermore, whereas most civil servants are transferred from time to time, many of the forest guards at Kakamega have been there for at least four years, and probably longer. Naturally they make friends in the area, and it is part of human nature to overlook the trespasses of one's friends. It is suggested that forest guards be transferred such that their tenure at any one place does not exceed five years. A final suggestion is that the forest guards be paid some sort of bonus for every cow arrested. The Department collects Kshs. 50 per head; why not turn Kshs. 5–10 over to the guard who arrested them? If financial incentive leads to more thorough patrol, the Department is likely to gain rather than lose revenue.

The number of people who hunt game is probably small, but their effect is large, since the animals they hunt are already extremely rare. It is unlikely that the people rely on game as food on a regular basis, since meat is available elsewhere, although of course at a cost. Again, regular patrols will help, and it is especially important that they encompass infrequently used trails, since this is where most traps are found. A bounty for traps recovered could be set, although this system could lead to misuse. At the same time, education should play a big part: the value of the game as something other than a source of protein, particularly as a source of revenue from tourist and research visitors, should be emphasized.

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Appendix I.

Checklist of native trees, woody vines, and shrubs of the Kakamega Forest.

ACANTHACEAE
Acanthus eminens C. B. Cl.
A. pubescens (Oliv.) Engl.
AGAVACEAE
Dracaena fragrans (L.) Ker-Gawl.
D. laxissima Engl.
ALANGIACEAE
Alangium chinense (Lour.) Harms
ANNONACEAE
Artabotrys likimensis De Wild.
A. monteiroa Oliv.
Monodora myristica (Gaertn.) Dun.
Uvariopsis congensis Robyns & Ghesq.

APPENDIX I. Continued.

APOCYNACEAE
Funtumia africana (Benth.) Stapf
Tabernaemontana ventricosa Hochst. ex DC.
Voacanga thouarsii Roem. & Schult.
ARALIACEAE
Polyscias fulva (Hiern) Harms
BIGNONIACEAE
Kigelia africana (Lam.) Benth.
K. moosa Sprague
Markhamia platycalyx (Bak.) Sprague
Spathodea campanulata P. Beauv.
Stereospermum kunthianum Cham.
BORAGINACEAE
Cordia africana Lam.
C. milleni Baker
CANELLACEAE
Warburgia salutaris (Bertol. f.) Chiov.
COMBRETACEAE
Combretum collinum subsp. *elgonense* (Exell) Okafor
Terminalia mollis Laws.
COMPOSITAE
Vernonia amygdalina Del.
CONNARACEAE
Agalaea ugandensis Schellenb.
EBENACEAE
Diospyros abyssinica (Hiern) White
EUPHORBIACEAE
Alchornea cordifolia (Schum. & Thonn) Muell. Arg.
A. laxiflora (Benth.) Pax & K. Hoff.
Bridelia micrantha (Hochst.) Baillon
Croton aliens Pax
C. macrostachyus Del.
C. megalocarpus Hutch.
C. sylvaticus Krauss
Drypetes gerrardii Hutch.
Erythrococca atrovirens (Pax) Prain
Macaranga kilimandscharica Pax
M. schweinfurthii Pax
Neoboutonia milleri (Muell. Arg.) Prain
Sapium ellipticum (Krauss) Pax
Securinega virosa (Willd.) Pax & K. Hoffm.
FLACOURTIACEAE
Casaeria battiscombei R. E. Fries
C. runssorica Gilg
Dovyalis macrocalyx (Oliv.) Warb.
Flacourtia indica (Burm. f.) Merrill
Oncoba routledgei Sprague
Rawsonia lucida Harv.
Trimeria grandifolia subsp. *tropica* (Burkill) Sleumer
GUTTIFERAE
Garcinia buchananii Bak. f.
HYPERICACEAE
Harungana madagascariensis Poir
ICACINACEAE
Apodytes dimidiata Arn.
LEGUMINOSAE (Caesalpinioideae)
Cassia didymobotrya Fres.
Piliostigma thonningii (Schumach.) Milne-Redh.
LEGUMINOSAE (Mimosoideae)
Acacia abyssinica Benth.
Albizia grandibracteata Taub.
A. gummifera (J. F. Gmel.) C. A. Sm.
Entada gigas (L.) Fewc. & Rendl.

APPENDIX I. Continued.

LEGUMINOSAE (Papilionoideae)
Craibia brownii Dunn
Erythrina abyssinica DC.
LOGANIACEAE
Anthocleista vogeli Planch.
Nuxia congesta Fresen.
LORANTHACEAE
Globimentula braunii (Engl.) Tiegh.
Phragmanthera dechallensis (Engl.) Polle
MALPIGHIACEAE
Flabellaria paniculata Cav.
MELIACEAE
Entandrophragma angolense (Welw.) C. DC.
Lepidotrichilia volkensii (Guerke) Leroy
Trichilia dregeana Sond.
T. emetica Vahl
Turraea holstii Guerke
MELIANTHACEAE
Bersama abyssinica subsp. *paullinioides* (Guerke) Verdc.
MORACEAE
Antiaris toxicaria (Pers.) Lesch.
Ficus exasperata Vahl.
F. kitubalu Hutch.
F. storthophylla Warb.
F. sur Forssk.
F. thonningii Blume
F. urceolaris Hiern
F. vallis-choudae Del.
Milicia excelsa (Welw.) Berg
Morus lactea (Sim) Mildbr.
Trilepisium madagascariense DC.
MYRSINACEAE
Embelia schimperi Vatke
Maesa lanceolata Forssk.
OCHNACEAE
Ochna insculpta Sleumer
Ouratea hiernsii (Van Tiegh) Exell
OLACACEAE
Strombosia scheffleri Engl.
OLEACEAE
Chionanthus mildbraedii (Gilg & Schellenb.) Stearn
Jasminum abyssinicum DC.
Olea welwitschii (Knobl.) Gilg & Schellenb.
POLYGALACEAE
Securidaca welwitschii Oliv.
PROTEACEAE
Faurea speciosa Welw.
RHAMNACEAE
Maesopsis eminii Engl.
Rhamnus prinoides L'Herit.
Scutia myrtina (Burm. f.) Kurz.
RHIZOPHORACEAE
Cassipourea ruwensoriensis (Engl.) Alston
ROSACEAE
Prunus africana (Hook. f.) Kalkm.
RUBIACEAE
Aulacocalyx dievilleoides (K. Schum.) Petit
Canthium guenzii Sond.
C. schimperanum A. Rich.
Chassalia cristata (Hiern) Brem.
Coffea eugenioides S. Moore
Craterispermum schwenfurthii Hiern
Gardenia jovis-tonantis (Welw.) Hiern

APPENDIX I. Continued.

Mussaenda arcuata Poir
M. erythrophylla Schumach. & Thonn.
Oxyanthus speciosus subsp. *stenocarpus* (K. Schum.) Bridson
Pavetta ternifolia (Oliv.) Hiern
Psychotria bagshawei Petit
Rothmannia urcelliformis (Hiern) Robyns
Rutidea smithii Hiern
R. syringoides (Webb) Brem.
Rytigynia butaguensis (De Wild.) Robyns
R. neglecta (Hiern) Robyns
Vangueria apiculata K. Schum.

RUTACEAE
Clausena anisata (Willd.) Benth.
Fagaropsis angolense (Engl.) Dale
Toddalia asiatica (L.) Lam.
Teclea grandifolia Engl.
T. nobilis Del.
Zanthoxylum gilletii (De Wild.) Waterman
Zanthoxylum mildbraedii (Engl.) Waterman
Z. rubescens Hook. f.

SAPINDACEAE
Allophylus macrobotrys Gilg
Blighia unijugata Baker
Dodonaea angustifolia L. f.
Lepisanthes senegalensis (Poir) Leenh.

SAPOTACEAE
Afrosersalisia cerasifera (Welw.) Aubrev.
Aningeria altissima (A. Chev.) Aubr. & Pellegr.
Bequaertiodendron oblanceolatum (S. Moore) Hiern & J. H. Hemsley
Chrysophyllum albidum G. Don
Manilkara butugi Chiov.

SOLANACEAE
Solanum aculeastrum Dunal
S. giganteum Jacq.

THYMELAEACEAE
Gnidia subcordata Meissn.

TILIACEAE
Triumfetta macrophylla K. Schum.

ULMACEAE
Celtis africana Burm. f.
C. mildbraedii Engl.
C. gomphophylla Bak.
Chaetacme aristata Planch.
Trema orientalis (L.) Blume

VERBENACEAE
Clerodendrum buchholzii Guerke
C. melanocrater Guerke
C. myricoides (Hochst.) Vatke
Lantana trifolia L.
Premna angolensis Guerke
Vitex doniana Sweet
V. fischeri Guerke

VITACEAE
Leea guineensis G. Don

APPENDIX II.

Common herbaceous flora of the Kakamega Forest complex (including pteridophytes).

DICOTYLEDONS

ACANTHACEAE
Acanthopale pubescens (Engl.) C. B. Cl.
Asystasia gangetica (L.) T. Anders.
A. schimperi T. Anders.
Brillantaisia madagascariensis Lindau
B. nyanzarum Burkill
Dicliptera laxata C. B. Cl.
Duvernonia, sp. nov.
Dyschoriste nobilior C. B. Cl.
D. perrottotii S. Moore
D. radicans Nees
Isoglossa oerstediana Lindau
Justicia betonica L.
J. pinguior C. B. Cl.
Phaulopsis imbricata (Forsk.) Sweet

AMARANTHACEAE
Achyranthes bidentata Schinz.
Celosia schweinfurthiana Schinz.

BALSAMINACEAE
Impatiens eminii Warb.
I. hochstetteri Warb.

CARYOPHYLLACEAE
Drymaria cordata (L.) Roem. & Schult.

COMPOSITAE
Adenostemma mauritianum DC.
Aspilia mossambicensis (Oliv.) Wild
Crassocephalum crepidioides S. Moore
C. montuosum (S. Moore) Milne-Redh.
C. vitellinum (Benth.) S. Moore
Dichrocephala integrifolia O. Kuntze
Helichrysum gerberifolium Sch. Bip.
H. panduratum O. Hoffm.
Inula decipiens E. A. Bruce
Melanthera scandens (Schumach. & Thonn.) Roberty var. *simplicifolia* Roberty
Mikania cordata B. L. Robinson
Sonchus luxurians (R. E. Fr.) C. Jeffrey
Spilanthes mauritiana (Pers.) DC.
Vernonia hymenolepis A. Rich.
V. tufnellii S. Moore

CONVOLVULACEAE
Dichondra repens J. R. & G. Forst.
Ipomoea involucrata Beauv.
I. sinensis (Desr.) Choisy subsp. *blepharosepala* (A. Rich.) Meeuse
I. tenuirostris Choisy

EUPHORBIACEAE
Acalypha brachystachya Horum.
A. ornata A. Rich.
Euphorbia inaequilatera Sond.

GENTIANACEAE
Sebaea grandis Steud.

LABIATAE
Achyrospermum parviflorum S. Moore
Becium sp.
Homalocheilos ramosissimum J. K. Morton
Leucas martinicensis R. Br.
L. micrantha Guerke
Ocimum lamiifolium Benth.
Orthosiphon rubicundud Benth.
Scutellaria paucifolia Baker

APPENDIX II. Continued.

LEGUMINOSAE (Papilionoideae)
Crotalaria pallida Ait.
C. recta A. Rich.
Desmodium repandum (Vahl) DC.
Indigofera volkensii Taub.
Trifolium baccarinii Chiov.
Vigna parkeri Bak.
Zornia pratensis Milne-Redh.
LORANTHACEAE
Globimetula braunii (Engl.) Tiegh.
Phragmanthera dschallensis (Engl.) Balle
MALVACEAE
Kosteletskya adoensis (A. Rich.) Mast.
MELASTOMATACEAE
Dissotis brazzae Cogn.
MENISPERMACEAE
Stephania abyssinica Walp.
MORACEAE
Dorstenia brownii Rendle
ONAGRACEAE
Ludwigia abyssinica A. Rich.
OXALIDACEAE
Biophytum petersianum Klotzsch
PIPERACEAE
Peperomia tetraphylla Hook. & Arn.
Piper capense L.
P. guineense Schumach. & Thonn.
POLYGALACEAE
Polygala petitiana A. Rich.
POLYGONACEAE
Polygonum setosulum A. Rich.
PRIMULACEAE
Ardisiandra wettsteinii R. Wagner
RUBIACEAE
Agathisanthemum globosum Hiern.
Oldenlandia herbacea (L.) Roxb.
O. monanthos (A. Rich.) Hiern.
Pentas decora S. Moore
Spermacoce pusilla Wall.
SCROPHULARIACEAE
Alectra sessiflora (Vahl.) Kuntze
Harveya sp.
UMBELLIFERAE
Centella asiatica (L.) Urb.
Hydrocotyle mannii Hook. f.
Sanicula elata Don.
URTICACEAE
Boehmeria platyphylla Don.
Elatostema orientale Engl.
Laportea alatipes Hook. f.
VERBENACEAE
Lippia carviodora Meikle
VITACEAE
Leea guineensis G. Don.

MONOCOTYLEDONS

ARACEAE
Culcasia scandens Beauv.
COMMELINACEAE
Commelina diffusa Burm. f.
Floscopa glomerata Hassk.
Pollia sp. (First record of the genus = *Kokwaro 4327*.)
GRAMINEAE
Brachiaria brizantha (A. Rich.) Stapf

APPENDIX II. Continued.

B. decumbens Stapf
B. umbratilis Napper
Cynodon dactylon Pers.
Digitaria velutina (Forssk.) P. Beauv.
Isachne mauritiana Kunth.
Loudetia kagerensis Hutch.
L. simplex (Nees) C. E. Hubbard
Oplismenus hirtellus (L.) Beauv.
Panicum calvum Stapf
Pseudochinolaena polystachya (H. B. & K.) Stapf
Setaria chevalieri Stapf & C. E. Hubbard
HYPOXIDACEAE
Hypoxis angustifolia Lam.
LILIACEAE
Chlorophytum macrophyllum Aschers.
ORCHIDACEAE (*restricted in Kenya to the Kakamega forest).
Aerangis kotschyana (Reichb. f.) Schltr.
A. rhodosticta (Kraenzl.) Schltr.
A. ugandensis Summerhayes
Angraecopsis amaniensis Summerhayes
A. gracillima (Rolfe) Summerhayes
**A. tenerrima* Kraenzl
Angraecum firthii Summerhayes
A. humile Summerhayes
A. sacciferum Lindl.
Ansellia africana Lindl.
A. gigantea Reichb. f. var. *nilotica* (Bak.) Summerhayes
Bolusiella imbricata (Rolfe) Schltr.
Brachycorythis buchananii (Schltr.) Rolfe
B. kalbreyeri Reichb. f.
B. ovata Lindl. ssp. *schweinfurthii* (Reichb. f.) Summerhayes
B. tenuior Reichb. f.
Bulbophyllum bequaertii De Wild.
B. cochleatum Lindl.
B. encephalodes Summerhayes
B. intertextum Lindl.
B. schlechteri De Wild.
Chamaeangis odoratissima (Reichb. f.) Schltr.
**Cyrtorchis brownii* (Rolfe) Schltr.
Disperis aphylla Kraenzl.
D. reichenbachiana Reichb. f.
Diaphananthe fragrantissima (Reichb. f.) Schltr.
D. lorifolia Summerhayes
Diaphananthe rutila (Reichb. f.) Summerhayes
D. xanthopollinia (Reichb. f.) Summerhayes
Eulophia angolensis (Lindl.) Reichb. f.
E. calantha Schltr.
E. chlorotica Kraenzl.
E. cucullata (Sw.) Steud.
**E. galeoloides* Kraenzl.
E. grantii (Reichb. f.) Summerhayes
E. orthoplectra (Reichb. f.) Summerhayes
E. shupangae (Reichb. f.) Kraenzl.
**E. stachyodes* Reichb. f.
**Habenaria egregia* Summerhayes
H. malacophylla Reichb. f.
Microcoelia guyoniana (Reichb. f.) Summerhayes
M. koehleri (Schltr.) Summerhayes
Nervillia kotschyi (Reichb. f.) Schltr.
Oberonia disticha (Lam.) Schltr.
Polystachia adansoniae Reichb. f.
P. cultriformis (Thou.) Spreng.

APPENDIX II. Continued.

P. fusiformis (Thou.) Lindl.
P. golungensis Reichb.
P. inconspicum Rendle
P. lindblomii Schltr.
P. spatella Kraenzl.
P. steudneri Reichb. f.
P. stricta Rolfe
Pteroglossaspis eustachya Reichb. f.
P. ruwenzoriensis Rolfe
Rangaeris brachyceras (Summerhayes) Summerhayes
R. muscicola (Reichb. f.) Summerhayes
Stolzia repens (Rolfe) Summerhayes
**Triceratorhynchus viridiflorus* Summerhayes
**Tridactyle anthomaniaca* (Reichb. f.) Summerhayes
**T. tridentata* (Harv.) Schltr.

PTERIDOPHYTES (Ferns and Fern Allies)

Species found only in the Kakamega Forest in Kenya.
Antrophyum mannianum Hook. (Vittariaceae)
Aspleninium angolense Bak. (Aspleniaceae)
A. blastophorum Hieron (Aspleniaceae)
A. ceii Pic. Ser. (Aspleniaceae)
A. formosum Willd. (Aspleniaceae)
A. pseudoauriculatum Schelpe (Aspleniaceae)
A. sp. A. (Aspleniaceae)
A. sp. D. (Aspleniaceae)
Bolbitis heudelotii (Fee) Alston (Lamariopsidaceae)
Ctenitis cirrhosa (Schumach.) Ching (Aspidiaceae)
Diplazium velaminosum (Diels) Pic. Ser. (Athyriaceae)
Dryopteris sp. A (Aspidiaceae)
Pteris mohasiensis Hieron (Adiantaceae)

Species found only in Kakamega and South Nandi Forests in Kenya.
Pteris preussii Hieron (Adiantaceae) (The commonest Pteris species in the forest.)

Species found in the Kakamega Forest and elsewhere in Kenya.
Adiantum hispidulum Swartz (Adiantaceae)
A. thalictroides Schlechtend (Adiantaceae)
Arthropteris orientalis (Gmel.) Posth. (Davalliaceae)
Asplenium aethiopicum (Burm. f.) Becherer (Aspleniaceae)
A. buettneri Hieron (Aspleniaceae)
A. cornutum Alston (Aspleniaceae)
A. dregeanum Kunze (Aspleniaceae)
A. elliottii C. H. Wright (Aspleniaceae)
A. erectum Willd. (Aspleniaceae)
A. inaequilaterale Willd. (Aspleniaceae)
A. lividum Kuhn (Aspleniaceae)
A. macrophlebium Bak. (Aspleniaceae)
A. mannii Hook. (Aspleniaceae)
A. protensum Schrad. (Aspleniaceae)
A. sandersonii Hook. (Aspleniaceae)
A. theciferum (Kunth) Mett. (Aspleniaceae)
A. unilaterale Lam. (Aspleniaceae)
Athyrium scandicinum (Willd.) Presl (Athyriaceae)
Cheilanthes bergiana Kunze (Adiantaceae)
C. farinosa (Forsk.) Kaulf. (Adiantaceae)
Coniogramme africana Hieron (Adiantaceae)

APPENDIX II. Continued.

Cyclosorus dentatus (Forssk.) Ching (Thelypteridaceae)
C. madagascariensis (Fee) Ching (Thelypteridaceae)
C. quadrangularis (Fee) Tard. (Thelypteridaceae)
C. sp. A (Thelypteridaceae)
Doryopteris concolor (Langsd. & Fisch.) Kuhn (Thelypteridaceae)
Drynaria volkensii Hieron (Polypodiaceae)
Dryoathyrium boryanum (Willd.) Ching (Athyriaceae)
Dryopteris manniana (Hook. f.) C. Chr. (Aspidiaceae)
Lomariopsis warneckei (Hieron) Alston (Lomariopsidaceae)
Loxogramme lanceolata (Swartz) C. Presl (Polypodiaceae)
Microlepia speluncae (L.) Moore (Dennstaediaceae)
Nephrolepis undulata (Swartz) J. Sm. (Davalliaceae)
Pellaea viridis (Forssk.) Prantl (Adiantaceae)
Phanerophlebia caryotidea (Hook. & Grev.) Copel (Aspidiaceae)
Pleopeltis macrocarpa (Willd.) Kaulf. (Polypodiaceae)
Pteridium aquilinum (L.) Kuhn (Dennstaediaceae)
Pteris buchananii Sim (Adiantaceae)
P. dentata Forsk. (Adiantaceae)
P. pteridioides (Hook.) Ballard (Adiantaceae)
P. vittata L. (Adiantaceae)
Pyrrosia schimperana (Mett.) Alston (Polypodiaceae)
Selaginella kraussiana (Kunze) A. Br. (Selaginellaceae)
Tectaria gemmifera (Fee) Alston (Aspidiaceae)
Thelypteris gueintziana (Mett.) Schelpe (Thelypteridaceae)
T. longicuspis (Bak.) Schelpe (Thelypteridaceae)
Trichomanes chevalieri Christ (Hymenophyllaceae)
T. melanotrichum Schlechtend. (Hymenophyllaceae)

APPENDIX III.

VERNACULAR NAMES OF TREES AND SHRUBS

I have used the term *Luhya* to cover all those dialects used in Western Province in reference to plant names found in the Kakamega Forest. A number of these plants also spread out of this forest and are found growing naturally in other parts of western Kenya. Similar vegetation is believed to have existed up to Gem area, including Yala town in Siaya District through Butere and Mumias in the presently thickly populated fertile land of both Nyanza and Western provinces. Although the local people have continued to clear the natural vegetation, there are still many similarities in the flora and vegetation of this area, which was once known as the Nyanza basin. The vegetation of Kakamega Forest is also close, although not entirely the same to that of the Nandi forests. This is probably duc to the fact that the latter are a little higher in altitude and hence have both the lowland tropical rain forest species as well as the highland forest species. Whereas the North Nandi Forest is distinctly separated from the Kakamega Forest by the Nandi escarpment, the South Nandi Forest

intermingles well with the southern portion of Kakamega Forest.

It is for these reasons that some common vernacular plant names in Nandi have been included in this report. In some of the existing literature (e.g., Dale & Greenway, 1961) plant names have been referred to as either Kakamega (a collection of vernacular names of plants from Kakamega area) or Kavirondo (unspecified languages spoken in the then Nyanza Province, including the present Western Province, which was known mainly as North Kavirondo). I have therefore attempted to separate strictly Luhya plant names from those of the neighboring tribes with which they sometimes share common boundaries and the same ecological zones. It should be noted that not all plants in the forest have local names. The following list therefore has primarily all the known Luhya names of trees and shrubs in Kakamega Forest, and in some cases the Nandi name when the tree also occurs in the Nandi Forests.

Amuutu. *Croton macrostachyus* (Euphorbiaceae), *Pavetta ternifolia* (Rubiaceae).
Apacha, **Apachi**. *Warburgia salutaris* (Canellaceae).
Asenuet. *Combretum collinum* (Combretaceae).
Chapchabayet. *Casaeria battiscombei* (Flacourtiaceae).
Chemsel. *Turraea holstii* (Meliaceae).
Chepkarelyon. *Trimeria grandifolia* subsp. *tropica* (Flacourtiaceae).
Chepkelelet, **Chepkeliliet**. *Celtis africana* (Ulmaceae).
Cheptuiyet. *Diospyros abyssinica* (Ebenaceae).
Chorwet. *Nuxia congesta* (Loganiaceae).
Embano. *Dracaena fragrans* (Agavaceae).
Eshimwani. *Garcinia buchananii* (Guttiferae).
Hukhulu. *Vitex fischeri* (Verbenaceae).
Ikahawa. *Coffea eugenioides* (Rubiaceae).
Ikhomo. *Chaetacme aristata* (Ulmaceae).
Ikoyi. *Artabotrys likinensis* (Annonaceae).
Inoyna. *Nuxia congesta* (Loganiaceae).
Irojo. *Trichilia emetica* (Meliaceae).
Itikwa. *Rutidea syringoides* (Rubiaceae).
Kabeya. *Oncoba routledgei* (Flacourtiaceae).
Kalembe. *Vitex doniana* (Verbenaceae).
Kapchobiriet, **Kaptouriet**. *Dovyalis macrocalyx* (Flacourtiaceae).
Keptangan. *Coffea engenioides* (Rubiaceae).
Kibabustainiet. *Maesa lanceolata* (Myrsinaceae).
Kipkumetiet. *Bersama abyssinica* (Melianthaceae).
Kipsebuet. *Neobontonia melleri* (Euphorbiaceae).
Kisambari. *Clausena anisata* (Rutaceae).
Kisangula. *Premna angolensis* (Verbenaceae).
Kisimbari. *Zanthoxylum mildbraedii* (Rutaceae).
Kitondo. *Tabernaemontana usambarensis* (Apocynaceae).
Kubusto. *Alangium chinense* (Alangiaceae).
Kumurembe. *Erythrina abyssinica* (Leguminosae subfam. Papilionoideae).
Kuriondet. *Teclea nobilis* (Rutaceae).
Kwamakonja. *Chaetacme aristata* (Ulmaceae).
Laburiko. *Lepidotrichilia volkensii* (Meliaceae).
Lichet. *Flacourtia indica* (Flacourtiaceae).
Likhomo. *Chaetacme aristata* (Ulmaceae).
Lirakalu. *Acanthus pubescens* (Acanthaceae).
Lisebesebe. *Maesa lanceolata* (Myrsinaceae).

APPENDIX III. Continued.

Luabare. *Toddalia asiatica* (Rutaceae).
Lubambo. *Nuxia congesta* (Loganiaceae).
Lubelakhaya. *Trilepisium madagascariensis* (Moraceae).
Lubinu. *Cassia didymobotrya* (Leguminosae subfam. Caesalpinioideae).
Luburika. *Rinorea brachypetala* (Violaceae).
Lubushi. *Momodora myristica* (Annonaceae).
Ludulio. *Manilkara butugi* (Sapotaceae).
Lugurek. *Mussaenda erythrophylla* (Rubiaceae).
Luhoiyahui. *Ficus storthophylla* (Moraceae).
Lukhonsongabu. *Canthium venosum* (Rubiaceae).
Lukhuba. *Dracaena fragrans* (Agavaceae).
Lukonsongabu. *Canthium gueinzii* (Rubiaceae).
Lumasai. *Harungana madagascariensis* (Hypericaceae).
Lumenenambuli. *Lantana trifolia* (Verbenaceae).
Lumenzani. *Turraea holstii* (Meliaceae).
Lusarari. *Lepidotrichilia volkensii* (Meliaceae).
Lusebi. *Canthium gueinzii* (Rubiaceae).
Luseno. *Ficus storthophylla* (Moraceae).
Lusesh. *Mussaenda erythrophylla* (Rubiaceae).
Lusiliru. *Oxyanthus speciosus* subsp. *stenocarpus* (Rubiaceae).
Lusiola. *Markhamia platycalyx* (Bignoniaceae).
Lusolokho. *Artabotrys likinensis* (Annonaceae).
Lusoroko. *Ficus storthophylla*, *Ficus urceolaris* (Moraceae).
Lusui. *Diospyros abyssinica* (Ebenaceae).
Mahorlu. *Stereospermum kunthianum* (Bignoniaceae).
Manamakulu. *Drypete gerrardii* (Euphorbiaceae).
Manguelo. *Rutidea smithii* (Rubiaceae).
Marakalu. *Acanthus pubescens* (Acanthaceae).
Marteet. *Cassipourea ruwensorensis* (Rhizophoraceae).
Mugangagu. *Gnidia subcordata* (Thymelaeaceae).
Murave. *Kigelia moosa* (Bignoniaceae).
Masaba. *Apodytes dimidata* (Icacinaceae).
Masineitet. *Croton megalocarpus* (Euphorbiaceae).
Mbalakhaya. *Trilepisium madagascariensis* (Moraceae).
Mbeshe. *Afrosersalisia corasifera* (Sapotaceae).
Mbulicha. *Cassipourea ruwensorensis* (Rhizophoraceae).
Mbulikha. *Rinorea brachypetala* (Violaceae).
Mkhulu. *Vitex doniana*, *V. fischeri* (Verbenaceae).
Mobet. *Markhamia platycalyx* (Bignoniaceae).
Mogoiwet. *Ficus sur* (Moraceae).
Morabe. *Kigelia africana* (Bignoniaceae).
Moykundi. *Bersama abyssinica* (Melianthaceae).
Msese. *Sapium ellipticum* (Euphorbiaceae).
Mshirakalu. *Rawsonia lucida* (Flacourtiaceae).
Msingo. *Ficus vallis-choudae* (Moraceae).
Mubuhu. *Neuboutonia milleri* (Euphorbiaceae).
Muendu. *Dodonaea viscosa* (Sapindaceae).
Mufutumwe. *Vitex fischeri* (Verbenaceae).
Mugonju. *Faurea rochetiana* (Proteaceae).
Muhandi. *Craibia brownii* (Leguminosae subfam. Papilionoideae).
Muhandu. *Craibia brownii* (Leguminosae subfam. Papilionoideae).

APPENDIX III. Continued.

Muhonji. *Terminalia mollis* (Combretaceae).
Muholu. *Vitex doniana, V. fischeri* (Verbenaceae).
Muhonde. *Craibia brownii* (Leguminosae subfam. Papilionoideae).
Muhunya. *Maesopsis eminii* (Rhamnaceae).
Muhutu. *Vitex fischeri* (Verbenaceae).
Mukaloho. *Cassipourea ruwensorensis* (Rhizophoraceae).
Mukanganya. *Bridelia micrantha* (Euphorbiaceae).
Mukangu. *Aningeria altissima* (Sapotaceae).
Mukhonzuli. *Albizia grandibracteata, Albizia gummifera* (Leguminosae subfam. Mimosoideae).
Mukoloho. *Cassipourea ruwensorensis* (Rhizophoraceae).
Mukoho, Mukuhakuha. *Macaranga kilimandscharica* (Euphorbiaceae).
Mukumasia. *Uvariopsis congensis* (Annonaceae).
Mukumari. *Cordia africana* (Boraginaceae).
Mukungu. *Aningeria altissima* (Sapotaceae).
Mukuyu. *Ficus sur* (Moraceae).
Mulama. *Piliostigma thonningii* (Leguminosae subfam. Caesalpinioideae).
Mulemwe. *Anthocleister vogelii* (Loganiaceae).
Mululu. *Chrysophyllum albidum* (Sapotaceae).
Mulundu. *Antiaris toxicaria* (Moraceae), *Trimeria grandifolia* subsp. *tropica* (Flacourtiaceae).
Mumandala. *Rothmannia urcelliformis, Aulacocalyx diervilleodes* (Rubiaceae).
Munamatolo. *Rawsonia lucida* (Flacourtiaceae).
Munamusai. *Harungana madagascariensis* (Hypericaceae).
Munamuveka. *Chassalia cristata* (Rubiaceae).
Mundana. *Leea guineensis* (Vitaceae).
Mungaliguru, Mungalikoro. *Premna angolensis* (Verbenaceae).
Munghambi. *Triumfetta microphylla* (Tiliaceae).
Mung'oma. *Cordia millenii* (Boraginaceae).
Munuku. *Morus lactea* (Moraceae).
Munyama. *Trichilia emetica* (Meliaceae).
Munyenya. *Acacia abyssinica* (Leguminosae subfam. Mimosoideae).
Murembe. *Erythrina abyssinica* (Leguminosae subfam. Papilionoideae).
Murengeritsa. *Craterispermum schweinfurthii* (Rubiaceae).
Murguiwet. *Olea welwitschii* (Oleaceae).
Murumba. *Milicia excelsa* (Moraceae).
Musaa. *Celtis gomphophylla* (Ulmaceae).
Musagala, Musakala. *Trema orientalis* (Ulmaceae).
Musamia. *Bequaertiodendron oblanceolatum* (Sapotaceae).
Musani. *Harungana madagascariensis* (Hypericaceae).
Musaretsi. *Lepisanthes senegalensis* (Sapindaceae).
Musasa. *Sapium ellipticum* (Euphorbiaceae).
Museno. *Ficus exasperata* (Moraceae).
Musesa. *Sapium ellipticum* (Euphorbiaceae).
Mushebeshebe. *Maesa lanceolata* (Myrsinaceae).
Mushema. *Sapium ellipticum* (Euphorbiaceae).
Musiema. *Trichilia dregeana* (Meliaceae).
Musila. *Harungana madagascariensis* (Hypericaceae).

APPENDIX III. Continued.

Musine. *Croton megalocarpus* (Euphorbiaceae).
Musinzi. *Trichilia emetica* (Meliaceae).
Musoso. *Sapium ellipticum* (Euphorbiaceae).
Musudzu. *Croton macrostachyus* (Euphorbiaceae).
Musuritsa. *Vernonia anygdalina* (Compositae).
Musutsu. *Croton macrostachyus* (Euphorbiaceae).
Mutaro. *Teclea nobilis* (Rutaceae).
Mutere. *Maesopsis eminii* (Rhamnaceae).
Mutobolo. *Alangium chinense* (Alangiaceae).
Mutondo. *Tabernaemontana usambarensis, Funtumia africana* (Apocynaceae).
Mutsudzu. *Croton sylvaticus* (Euphorbiaceae).
Mutsurio. *Spathodea campanulata* (Bignoniaceae).
Mutsutsu. *Croton sylvaticus* (Euphorbiaceae).
Mutsutsu-munamulira. *Alchornea laxiflora, Croton sylvaticus* (Euphorbiaceae).
Mutukuyu. *Olea welwitschii* (Oleaceae).
Mwadzi, Mwanzu, Mwatsi. *Polyscias fulva* (Araliaceae).
Mweye, Mweyu. *Celtis africana* (Ulmaceae).
Mwieniet. *Dovyalis macrocalyx* (Flacourtiaceae).
Mwiritsa. *Prunus africana* (Rosaceae).
Namasinzi. *Casaeria battiscombei* (Flacourtiaceae).
Namasinzi. *Oxyanthus speciosus* subsp. *stenocarpus* (Rubiaceae).
Noioet. *Fagaropsis angolense* (Rutaceae).
Olokhongwe. *Terminalia mollis* (Combretaceae).
Olosulolyo. *Alchornea cordifolia* (Euphorbiaceae).
Olulaha. *Combretum collinum* (Combretaceae).
Olumulusya. *Vernonia anygdalina* (Compositae).
Oluseshe. *Jasminum abyssinicum* (Oleaceae).
Omufutu. *Vitex doniana, V. fischeri* (Verbenaceae).
Omuhuru. *Vitex fischeri* (Verbenaceae).
Omutembe. *Erythrina abyssinica* (Leguminosae subfam. Papilionoideae).
Omutukuyu. *Olea welwitschii* (Oleaceae).
Pepterit. *Lantana trifolia* (Verbenaceae).
Ratinuet. *Kigelia africana* (Bignoniaceae).
Ruandet. *Canthium schimperanum* (Rubiaceae).
Sagawatiet. *Zanthoxylum gilletii* (Rutaceae).
Saiyet. *Polyscias fulva* (Araliaceae).
Samotet. *Cordia africana* (Boraginaceae).
Se. *Albizia grandibracteata* (Leguminosae subfam. Mimosoideae).
Sebesebet. *Macaranga kilimandscharica* (Euphorbiaceae).
Sebetaiyet. *Spathodea campanulata* (Bignoniaceae).
Senetuet. *Cassia didymobotrya* (Leguminosae subfam. Caesalpinioideae).
Set. *Albizia grandibracteata, A. gummifera* (Leguminosae subfam. Mimosoideae).
Seyet. *Albizia grandibracteata, A. gummifera* (Leguminosae subfam. Mimosoideae).
Shekoye. *Canthium schimperanum* (Rubiaceae).
Shetoto. *Pavetta ternifolia* (Rubiaceae).
Shiarambatza. *Blighia unijugata* (Sapindaceae).
Shiboyirambaku. *Piliostigma thonningii* (Leguminosae subfam. Caesalpinioideae).
Shigulotso. *Fagaropsis angolense* (Rutaceae).
Shigulutsu. *Zanthoxylum rubescens* (Rutaceae).
Shigumaha. *Clerodendrum myricoides* (Verbenaceae).

APPENDIX III. Continued.

Shihanga. *Mussaenda arcuata* (Rubiaceae).
Shikanganya. *Bridelia micrantha* (Euphorbiaceae).
Shikhomoli. *Vangueria apiculata* (Rubiaceae).
Shikhuma. *Zanthoxylum gillettii* (Rutaceae).
Shikoye. *Canthium schimperanum* (Rubiaceae).
Shikulakuli. *Phragmanthera rufescens* (Loranthaceae).
Shikunga. *Chaetacme aristata* (Ulmaceae).
Shikuma. *Clerodendrum myricoides* (Verbenaceae).
Shimwani. *Coffea eugenioides* (Rubiaceae).
Shinakutorio, **Shinapateria**. *Dovyalis macrocalyx* (Flacourtiaceae).
Shingulutsi. *Clausena anisata* (Rutaceae).
Shirakali. *Oncoba routledgei* (Flacourtiaceae).
Shirietso. *Erythrococca atrovirens* (Euphorbiaceae), *Turraea holstii* (Meliaceae).
Shiriezo. *Dovyalis macrocalyx* (Flacourtiaceae).
Shirikamabinga. *Bersama abyssinica* (Melianthaceae).
Shirimbadsi. *Zanthoxylum milidbraedii* (Rutaceae).
Shishimbari. *Clausena anisata* (Rutaceae).
Shitondo. *Pavetta ternifolia* (Rubiaceae), *Tabernaemontana usambarensis* (Apocynaceae).

APPENDIX III. Continued.

Shitoto. *Pavetta ternifolia* (Rubiaceae).
Shiunza. *Celtis mildbraedii* (Ulmaceae).
Shiviambinga. *Bersama abyssinica* (Melianthaceae).
Shughoma. *Zanthoxylum rubescens* (Rutaceae).
Shunghung'ung'ani. *Coffea eugenioides* (Rubiaceae).
Shunza. *Celtis mildbraedii* (Ulmaceae).
Sibuhu. *Macaranga schweinfurthii* (Euphorbiaceae).
Sigergangan. *Coffea eugenioides* (Rubiaceae).
Simbari. *Zanthoxylum mildbraedii* (Rutaceae).
Sinamagulu. *Drypetes gerrardii* (Euphorbiaceae).
Soget. *Warburgia salutaris* (Canellaceae).
Tebesuet. *Croton macrostachyus* (Euphorbiaceae).
Tegeldet, **Tegelitet**. *Acanthus pubescens* (Acanthaceae).
Tsikhulumuru. *Afrosersalisia cerasifera* (Sapotaceae).
Tsindaha. *Combretum collinum* (Combretaceae).
Tungururiet. *Flacourtia indica* (Flacourtiaceae).
Twendet. *Prunus africana* (Rosaceae).
Umufutumbwe. *Vitex fischeri* (Verbenaceae).
Wanda. *Apodytes dimidiata* (Icacinaceae).

PRACTICAL ASPECTS OF MOIST FOREST CONSERVATION IN TANZANIA[1]

JON C. LOVETT[2]

ABSTRACT

The importance of conserving the moist forests of Tanzania is discussed from an economic, social, and scientific perspective. The forests are especially significant for their high degree of endemism but also as areas of water catchment, a habitat for numerous plant and animal species, and as a genetic resource of economically important plants. Important economic endemics include species of horticultural interest such as *Saintpaulia*, timber trees such as *Cephalosphaera*, and wild relatives of crop plants such as *Coffea*. Factors necessary for the conservation of the Tanzanian moist forests are wide-ranging and include education, the establishment of building pole and fuelwood plantations, and the definition of the more important areas for concentrated conservation efforts. The preparation of field guides is identified as an area where botanists can help with practical conservation.

RÉSUMÉ

L'importance de la conservation des forêts humides en Tanzanie est exposée d'un point de vue économique, social, et scientifique. Ces forêts sont particulièrement remarquables par leur taux élevé d'endémisme et leur capacité de rétention de l'eau; en outre, elles servent d'habitat pour de nombreuses éspèces de plantes et d'animaux et constituent une ressource génétique de plantes d'importance économique. Parmi ces endémiques on peut signaler des éspèces d'un intérêt horticultural (e.g., *Saintpaulia*), des arbres utilisés pour leur bois (e.g., *Cephalosphaera*) et des éspèces sauvages proches de plantes cultivées (e.g., *Coffea*). Les facteurs importants pour la conservation des forêts humides de Tanzanie sont nombreux: programmes éducatifs; l'installation de plantations pour la production de bois de construction et de chauffage; la définition des régions à conserver prioritairement. Les botanistes peuvent oeuvrer utilement à cette conservation par la préparation de guides pratiques de terrain.

The moist forests of Tanzania, particularly those on the mountains and coast in the east of the country, are exceptionally rich in endemic genera and species in comparison to other places of similar size in tropical Africa. Consequently, they have been selected by the International Union for Conservation of Nature and Natural Resources (IUCN) as some of the 150 areas worldwide containing important ecosystems for conservation (Droop, 1988). But the conservation of the moist forests of Tanzania is not without its problems.

The population growth of sub-Saharan Africa has been reviewed recently by Goliber (1985). The outlook for population increase keeping within bounds determined by the local environment under current land use systems is bleak. The population of sub-Saharan Africa is increasing at 3.1% per year, compared to 1.8% in Asia and 2.4% in Latin America. Yet since the 1960s the region has become the only one in the world where food production is losing the race with population growth.

In Tanzania the population is currently estimated to be about 21.7 million and increasing at a rate of 3.5% per year. To put the percentage population increase into perspective, the population of Tanzania doubled between 1958 and 1978, rising from about 9 million to over 18 million. It is projected that Tanzania will have 39.1 million people by the year 2000 and 83.8 million by 2025 (Goliber, 1985). However, it is thought that these projections will never be realized. Before such figures are reached, the population-induced environmental degradation would lead to economic decline, social disintegration, and the inevitable rise in death rates (Brown, 1985).

The role of conservation in countries such as Tanzania must be seen in the perspective of population increase and consequent environmental degradation. The people of Tanzania essentially need two commodities, wood and water, both of which are found in and come from the forests. The conservation of forests may well prove to be crucial in preventing the environmental deg-

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radation and consequent human suffering that already exists in some parts of Africa.

The United Nations Food and Agriculture Organization (FAO, 1979) estimate that 99% of all wood cut in Tanzania is burnt as domestic fuel, and in the ten years between 1968 and 1979 there was a 38% increase in wood consumption. In area terms, the natural woodlands, rather than the forest, are bearing the brunt of the demand for firewood. It is estimated that the annual proportion of woodland cleared is as high as 55% in Kilimanjaro region and 30% in Mara and Mwanza regions. In areas such as Kilimanjaro, Zanzibar, and Pemba it is thought that population densities by 1995 will be so high that techniques such as agroforestry will not be able to provide the fuel wood needed because of land scarcity (Hall, 1984). In the moist forests in areas of high population density such as the Usambara, large forest trees are being felled and left to dry purely for firewood (pers. obs.), as all the available natural dead wood has been gathered. In other areas, such as the Pugu Hills near Dar es Salaam, clearance of moist forest for charcoal is an extremely serious threat (Hawthorne, 1984; Howell, 1981), since Tanzania's largest city relies heavily on charcoal for fuel. The other main use of wood in Tanzania is for building. Wood extracted from the forests for this purpose not only includes large timber trees but also considerable quantities of small diameter poles for hut building (Rodgers & Hall, 1986). In many moist forests the collection of poles has reached such an extent that there is little regeneration of canopy tree species.

The importance of the second essential commodity, water, cannot be underestimated. The rapidly increasing population of Tanzania, dependent largely on subsistence agriculture, needs food, and to grow that food it needs water. Tanzania is a predominantly dry country. Nearly half the land area receives less than 760 mm of rain a year in four years out of five (i.e., reliable rain), and 96% of the country receives less than 1,270 mm of reliable annual rain (Griffiths, 1972). However, there are limited areas of high rainfall, which can receive as much as 3,000 mm a year. The highest population densities in Tanzania (outside urban areas) are found in these places. Most of the high rainfall areas are on steep slopes, and massive soil erosion has followed forest clearance for cultivation (Temple & Rapp, 1972). More disturbing than the loss of soil fertility due to erosion is the possibility of loss of dry season flow from the high rainfall mountain catchment areas due to deforestation and the destructive floods that originate in denuded catchments during the rains.

Importance of the Moist Forests of Tanzania

In addition to its vital role in water catchment and soil conservation, the forest is valuable as a genetic resource, both for local use and as a potential source of cash crops. The moist forests of Tanzania have a high degree of endemism. The mountain forests have an estimated 25% of their species restricted to Tanzania, and a higher percentage of species occur in the Tanzanian forests and in adjacent southeast Kenya and northern Malawi (Lovett, 1988). Similarly, the coastal forests of Tanzania have a high number of both species and generic endemics (Hawthorne, 1984). The forests are of great scientific interest, and through studying them we will be able to better understand the climatic changes and evolutionary processes that have led to the present-day flora. Unfortunately, due to the population pressures discussed above, there is little room for argument that the forests should be conserved for the purposes of scientific study alone.

The flora is of more importance than for pure scientific research. Many of the forest plants are used by local people for medicinal purposes (Kokwaro, 1976; Watt & Beyer-Brandwijk, 1962; Haerdi, 1964) as well as for building poles and the production of household implements. In many areas of Tanzania modern medication is either not available or too expensive, and so herbal preparations are often the only means of combating sickness. This is not to say that these preparations are not effective; it is likely that many of the plants contain pharmaceutically active compounds that could benefit mankind as a whole. With the high degree of endemism in the forests, the pharmaceutical potential of the plants restricted to Tanzania that are used medicinally may be considerable. Some 40% of the world's drug sales come from natural sources, generating world commercial sales of about $40 billion annually (Synge, 1984).

Timber from the forests is used extensively for local construction and is often cut illegally from forest reserves. The profits to be made from timber extraction from the indigenous forests are high, as there is great demand for building wood suitable to local conditions. There is no shortage of plantation-grown building wood in Tanzania,

as there are large areas of pine plantation. However, to withstand termite attack the pine must be chemically treated, which is expensive and requires imported chemicals. In contrast, the indigenous timber trees are more resistant to termite attack.

Many timber trees are endemic or nearly so. For example, *Beilschmeidia kweo* (Mildbr.) Robyns & Wilczek (Lauraceae) is endemic in the Afromontane and Transitional rain forests (sensu White, 1983) of the Eastern Arc mountains (sensu Lovett, 1988). This species was so heavily logged in the early part of this century that in 1949 Brenan and Greenway wrote of it: "An economic timber before 1914, exported to Germany where it was used for waggon and ship building, but supplies now exhausted" (Brenan & Greenway, 1949). There is a danger here of repeating the genetic impoverishment seen with the overexploitation of *Swietenia mahogoni* (L.) Jacq. (Meliaceae) in Central America (Pennington & Styles, 1981). Other endemic timbers are *Isoberlinia scheffleri* (Harms) Greenway (Leguminosae, Caesalpinoideae) and the monotypic genus *Cephalosphaera*. The single species *C. usambarensis* (Warb.) Warb. (Myristicaceae) is exploited heavily for the production of plywood and veneer and responds readily to plantation cultivation. It must also be remembered that the forests in the east of Tanzania have been isolated from other forest areas for a very long time (Lovett, 1988). Even widespread timber species that also occur in the forests of Tanzania are likely to have distinct genotypes due to their prolonged isolation. Hence, the eastern Tanzania forests are likely to be an important provenance of many more widely distributed species. Despite the fact that they are slow growing in comparison to exotic pines, the indigenous hardwoods may become important plantation species due to their resistance to termite attack and export potential.

Some endemic Tanzanian trees used for timber also yield other products. For example, *Allanblackia stuhlmannii* (Engl.) Engl. (Guttiferae) produces large fruits weighing up to seven kilograms, with seeds containing about 70% extractable fat of high molecular weight suitable as a base for the manufacture of soap and candles (Lovett, 1983).

Another potentially important genetic resource in the Tanzanian moist forests are the indigenous species of *Coffea*. Of the 23 species of *Coffea* that occur in east and southern Africa, 16 occur in Tanzania. Of these, nine are too poorly known to be described, 10 are not known outside Tanzania at species level (including the poorly known species), and one is not known outside Tanzania at subspecies level. Three of the Tanzanian species have already been used to make coffee (Bridson, 1982). There are an estimated 40 species of *Coffea* in the world (Airy Shaw, 1980), thus 40% of the world's species of *Coffea* occur in Tanzania, 25% of which occur nowhere else.

The current annual world trade of coffee is about 3.6 million tons, which was valued at $12,000 million at 1981 prices (Marshall, 1985). Unfortunately, the crop suffers from a variety of diseases that can reduce the yield by as much as 50–80% (van der Vossen, 1985). If resistance to these diseases can be bred into commercial coffee varieties from the wild species, then yields can be improved. As coffee exports are controlled on a quota basis from producer countries, the actual amount of coffee exported cannot be increased from any one producer. However, if yields are improved, then prime agricultural land currently under coffee can be used to produce food for the rapidly increasing population of many of the producer nations. Coffee is one of Tanzania's most important export crops in terms of foreign exchange earned (Tanzania, 1976) and occupies much wet and fertile land on the volcanic soils in the north of the country.

Possibly as familiar as coffee in the developed world is *Saintpaulia ionantha* H. Wendl. (Gesneriaceae), an economically important endemic to the forests of eastern Tanzania and known in the horticultural trade as the African violet. Eighteen of the 20 known species of *Saintpaulia* are endemic to eastern Tanzania, and the genus is endemic to southeast Kenya and Tanzania. Genetically very plastic, many commercial varieties have been produced from the limited wild stock in cultivation, and the retail trade is worth an estimated $30 million a year (Lovett, 1984). Even more possibilities remain, including the potential for the production of a hardy variety from species such as *Saintpaulia goetzeana* Engl., which grows at 2,000 m in the forests of the Uluguru mountains of Tanzania and experiences occasional frosts.

Two other genera with great horticultural potential that are well-represented in Tanzanian moist forests are *Impatiens* (Balsaminaceae) and *Streptocarpus* (Gesneriaceae). Of the 109 species of *Impatiens* that occur in Africa, 53 grow in Tanzania, and of these, 27 are endemic to Tan-

zania (Grey-Wilson, 1980). Twenty-two species of *Streptocarpus* grow in Tanzania, of which 13 are endemic. There are approximately 130 species of *Streptocarpus* worldwide, so about 10% of the total number of species in the genus are endemic to Tanzania (Hilliard & Burtt, 1971).

The subject of practical aspects of in situ conservation of forest genetic resources has long been overlooked. An FAO committee to study the matter of forest genetic resource conservation created in 1968 has taken 17 years to propose guidelines for the in situ conservation of forest genetic resources (Roche & Dourojeanni, 1984) despite calls for a recognition of their importance (Roche, 1975a) and the recommendation that "in situ conservation is the ideal form of conservation of whole ecosystems, and should be implemented wherever practicable" (Roche, 1975b). In contrast to its recommendations to conserve forests, the FAO has also produced a book in Swahili on how to log natural forests using chainsaws (FAO, 1980). Such contradictions need to be examined closely.

Inputs Needed to Conserve the Tanzanian Moist Forests

From the preceding sections it is obvious that the moist forests of Tanzania are of considerable social and economic importance, both for their role in water catchment and as a genetic resource. Due to the varied nature of the topography and local climate, in addition to human disturbance, the forests are often fragmented, and some forest areas may be relatively small in extent, probably too small to allow limited management. A system of strict nature reserves needs to be established to protect as much important forest as possible. The management of such reserves has been reviewed recently by Hall (1983), who points out that considerable inputs are required to protect such areas, a fact often ignored by foresters. In Tanzania in particular, the forests are under considerable pressure, primarily as a result of rapid population increase.

This presents considerable practical problems to the conservation of the forests, as the land on which the forests stand is in ever-increasing demand for agriculture despite the fact that the loss of the forests will be detrimental to the long-term agricultural productivity. As a result, the efforts needed to save the forests from degradation and eventual destruction are multidisciplinary and expensive.

Perhaps one of the first requirements is a program of education on the importance of the forests. This not only needs to be directed at the young people who will inherit the natural resources of Tanzania but also at those currently in positions of authority whose decisions affect the forests. For example, a Finnish consulting company employed by the Finnish government recently recommended that large areas of Tanzanian moist forest be felled for timber (Jaako Poyry, 1980). The reasoning behind this recommendation is not clear. This type of asset stripping is more commonly associated with profit-making multinational companies who have no long-term interest in the country they are exploiting. The timber that it was proposed to exploit is in forest reserves created for the long-term protection of water catchment areas.

The Tanzanian government is aware of the importance of education in the conservation of its natural resources and there is a "Forests Are Wealth" campaign designed to promote awareness of the importance of the country's forests and encourage the planting of trees. Unfortunately, the campaign is being hindered by lack of resources, although it has achieved marked success in its main aims within the financial constraints of its operation (Tanzania, 1982).

Although local people may be aware of the importance of the forests through education, they will still need the commodities such as firewood and building poles which were previously obtained from the forest. An alternative source must therefore be provided in the form of plantations of suitable species of sufficient size to allow for increases in the population. The Tanzanian government is actively promoting suitable village forestry schemes and has produced a valuable guide to techniques and species selection for village forestry (Tanzania, 1984). The provision of these plantations means that potential agricultural land will be utilized for purposes other than food production. Consequently agricultural techniques need to be improved to increase the food production from the existing area under agriculture. For example, contour planting of fodder crops such as Guatemala grass can reduce soil erosion in addition to providing food for domestic stock that may otherwise overgraze natural vegetation. This approach is being adopted in areas of high population density such as the Usambara Mountains by a West German assisted and funded aid project, the Tanga Integrated Rural Development Project (TIRDEP). Such aid

projects are expensive and slow to implement and so do not have the glamour of the building of factories, roads, or large dams, where much of the financial assistance is used to import equipment and expertise from the donor country.

Important areas of forest also need to be defined, both in terms of their significance as water catchments and as genetic resources. Forested water catchments need to be protected in areas of high rainfall with steep slopes, both to maintain dry season flow and to prevent flooding during the rains. Areas of high genetic diversity are more difficult to define, as we still know comparatively little about what the different areas of forest contain, although there is an excellent basis for endemic species-rich site selection (Polhill, 1968).

Recently, increasing interest in the Tanzanian forests has resulted in a number of publications (for review see Rodgers & Homewood, 1982). Funding has also been provided by the World Wildlife Fund for fieldwork as part of its Tropical Forests and Primates campaign, in addition to fieldwork by students and staff of the Sokione University forestry faculty at Morogoro in Tanzania (Hall, 1985) and other institutions such as Uppsala and Oxford Universities (Hawthorne, 1984). This work has been aimed primarily at classifying the woody vegetation of the forests using quantitative techniques and the preparation of checklists of different forest areas.

The use of quantitative techniques for classifying the vegetation is particularly important, as variation in topography, local climate, and soils has resulted in many different forest types. African forest classification has been improved through a phytogeographic approach (White, 1983), but a finer scale is required for the needs of conservation. For example, the Tanzanian volcanic mountains have a markedly different forest type than the ancient crystalline mountains, yet both are classified as Afromontane Rain Forest by White (1983).

Future Work

The problems of moist forest conservation in Tanzania are manifold. Botanists may not be able to help directly in agricultural improvement, plantation forestry, or the hydrological assessment of water catchments, but their ability is vital to the production of floras that can be used in the field. The existing Tanzanian floras are either out of date (Brenan & Greenway 1949) or incomplete and difficult to use (*Flora of Tropical East Africa*: Milne-Redhead et al., 1952 to date). Until there is a field guide to the identification of moist forest species, much of the work of practical value to conservation—such as a study of regeneration of indigenous trees in natural forest—is extremely difficult. More importantly, Tanzanian foresters and botantists need to be able to identify the plants growing in their own country without having to send material to foreign herbaria.

The usefulness of a field guide is increased if it is accompanied by descriptions of the forest and its environment such as that produced for Malawi (Chapman & White, 1970). Such works are rare for tropical Africa, and although they will not solve the problems of population pressure and forest destruction, they will lead work that will develop a better understanding of the forests. This in turn will help with conservation.

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THE SEED STRUCTURE OF *NAUCLEA POBEGUINII* (POBÉG. EX PELLEGRIN) PETIT

DANIEL K. ABBIW[1]

Of the five species of *Nauclea* in tropical West Africa, three are represented in Ghana: *N. diderrichii* ("Kusia"), *N. Pobeguinii* ("Sukusia"), and *N. latifolia* ("Sukisia," African peach). A fourth species, *N. vanderguchtii,* is recorded from southern Nigeria and the Ivory Coast; a fifth, *N. xanthoxylon,* is reported from the Ivory Coast in *La Flore Forestière de la Côte d'Ivoire* (Aubreville, 1959) but not recorded in the *Flora of West Tropical Africa* (Hutchinson & Dalziel, 1963).

Nauclea latifolia is a savanna plant, a straggling shrub to a small tree about four meters high, occurring in both the southern and northern savanna zones of the country. It is fairly common and distinct in habit and habitat from the remaining two, both high forest trees and superficially similar. *Nauclea diderrichii* grows to a height of about 40 m and *N. pobeguinii* to about 31 m. *Nauclea diderrichii* is more frequent than *N. pobeguinii.* Frequencies given by Taylor (1960) from enumeration surveys are presented in Tables 1 and 2. According to these figures, *Nauclea diderrichii* is found throughout the forest zone and is well represented, but *N. pobeguinii* is uncommon. In addition to the two habitats given in Table 2, it has been recorded from the Pamu-Berekum and Aiyaola Forest Reserves. The single vegetative specimen in the Ghana Herbarium, *Hall 3347,* was collected from Nsuaem on the Agona Junction–Tarkwa Road. Irvine (1961) gives the distribution as Ivory Coast to Nigeria, Malawi, and Mozambique.

TABLE 2. Results of enumeration surveys for *Nauclea pobeguinii* (from Taylor, 1960).

Forest Reserve	Acres Enumerated	Girth Classes (in ft.)			
		3–5	5–7	7–9	9–11
Ankasa	120	2	4	1	—
Esukawkaw River	1,440	11	6	6	2

SEED CHARACTER

Nauclea has small seeds embedded in a peach-like fruit. Ridsdale & van den Brink (1975) described the seeds as ovoid to ellipsoid, sometimes slightly bilaterally compressed, not alate. Aubreville (1959) gives the size as 2 mm long.

To collect the seeds, the ripe fruits were macerated in water. The fruits of *Nauclea latifolia,* which grows around the University of Ghana Legon, were first collected and macerated. Later the fruits of *N. diderrichi* and *N. pobeguinii* were collected in the Aiyaola Forest Reserve near the University of Ghana Agricultural Research Station at Kade. The fruits of *N. diderrichii* were also macerated, the water and fruit pulp poured off, and the seeds collected. Then the fruits of *N. pobeguinii* were macerated and the water and fruit pulp poured off, but there were no seeds at the bottom of the container. They had been poured off with the water. The seeds of *N. pobeguinii,* unlike the other two, float in water.

TABLE 1. Results of enumeration surveys for *Nauclea diderrichii* (from Taylor, 1960).

Forest Reserve	Acres Enumerated	Girth Classes (in ft.)				
		3–5	5–7	7–9	9–11	11+
Subri	965	14	28	28	15	4
Fure	381	4	29	38	29	7
Bia South	734	35	29	13	6	2
Ayum	306	12	5	2	14	2
Atewa Range	573	17	29	30	24	12

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Discussion

Nauclea pobeguinii is a tree of moist situations—marshes and flooded forest—the floating seeds probably being an adaptation to dispersal, which explains its distribution along streams whenever it occurs. Further research is required to establish whether other species of *Nauclea* with a similar habitat to *N. pobeguinii* have floating seeds.

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STRATEGIES IN CHROMOSOME EVOLUTION IN *PELARGONIUM* (GERANIACEAE)[1]

F. Albers[2]

Abstract

Chromosome studies in *Pelargonium* L'Hér. have shown that the sections of the genus have different karyological strategies. Section *Pelargonium,* containing several morphologically primitive species, possesses the basic chromosome number $x = 11$. This diploid karyotype is considered to be primitive. Half of the species of the section are diploid, the other half includes tetraploid, hexaploid, and octoploid species in a polyploid series from 22 to 88. Section *Ligularia* comprises woody or herbaceous subshrubs and is considered advanced. In this section the basic number $x = 11$ is also found, but the chromosomes are larger. Besides species with $2n = 22$, there are diploid species with $2n = 20$, 18, and 16, which form a descending dysploid series. There are also a few tetraploids on the base of $x = 8$ and 9. Some remarks on the distribution range of the cytotypes are made.

Résumé

Des études cytotaxonomiques du genre *Pelargonium* L'Hér. montrent que les sections dans le genre suivent des stratégies karyologiques différentes. La section *Pelargonium,* qui contient plusieurs espèces morphologiquement primitives, possède $x = 11$ comme nombre de base de chromosomes. Ce karyotype diploïde est considéré primitif. Une moitié des espèces de la section est diploïde, l'autre moitié comprend des espèces tetra-, hexa-, et octoploïdes, qui forment une série polyploïde: 22, 44, 66, 88. La section *Ligularia* comprend des arbustes ligneux ou herbacés et doit être considerée comme une section avancée. Dans cette section le nombre de base est aussi 11, mais les chromosomes sont bien plus grands. Outre des espèces avec $2n = 22$, il y a des espèces diploïdes avec $2n = 20$, 18, et 16 qui forment une série descendante. Il y a quelques tetraploïdes basées sur $n = 8$ et 9. L'auteur fait des remarques sur l'echelle de répartition des cytotypes.

A taxonomic revision of *Pelargonium* was recently begun by van der Walt and his coworkers at Stellenbosch University, South Africa, and their morphological, anatomical, palynological, and ecological studies (van der Walt, 1977; van der Walt & Vorster, 1981, 1983) are now being complemented by cytotaxonomy. Several chromosome counts have been reported in the genus *Pelargonium,* especially among horticultural and commercial taxa (Knicely, 1964; Daker, 1967, 1969; Tokumasu, 1974; Payet, 1982; Yu & Horn, 1984). Earlier chromosomal observations of Gauger (1937) and Warburg (1938) are of lesser value because both authors studied cultivated plants from botanic gardens. Recent chromosome counts have been determined from field-collected and cultivated plants of known localities (Gibby & Westfold, 1983; Albers & van der Walt, 1984).

Pelargonium was last revised by Knuth (1912), who divided the genus into 15 sections. Van der Walt & Vorster (1983) completed this classification by adding a sixteenth monotypic section, although van der Walt (1977) expressed doubt about whether the division of species into sections reflects their natural relationships. This is one of the problems in interpreting the chromosome numbers.

The lowest diploid chromosome number so far recorded is $2n = 8$ in *Pelargonium elongatum* (section *Eumorpha*) (Gibby & Westfold, 1983). Other low numbers in several species are $2n =$ 16, 18, 20, and 22. Although this appears to be an ascending series after a doubling of the 8-genome, another fact must be taken into consideration. Daker (1969) observed that all genomes with the basic number 10 and 11 comprise small chromosomes and those with $n = 8$ and 9 comprise large chromosomes. This, however, is not correct. After studying nearly half the species, I have found none with $n = 10$ and small chromosomes; all species with this number have chromosomes of the larger type.

In the species with the basic number $x = 11$,

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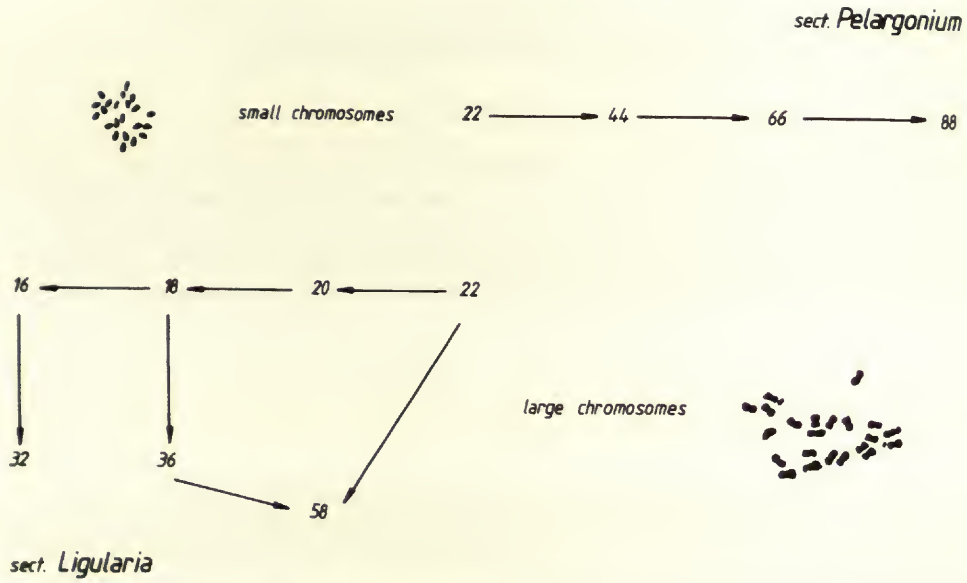

FIGURE 1. Chromosome numbers in two sections of *Pelargonium*, section *Pelargonium* and section *Ligularia*.

genomes with small as well as larger chromosomes can be found. Species with smaller chromosomes belong in sections *Pelargonium* and *Glaucophyllum* (Albers & van der Walt, 1984). Section *Pelargonium* is considered to be the most primitive in the genus, and four of the five species in section *Glaucophyllum* have some morphological characters similar to section *Pelargonium*. Their relationship is also supported by the occurrence of natural hybrids between species of the two sections (van der Walt & Vorster, 1983). In one other section, *Eumorpha*, there are three species with small chromosomes (Gibby, pers. comm.), whereas the majority of the species has large chromosomes.

Half of the species of section *Pelargonium* and all seven species of the other sections with small chromosomes of 1.0–1.5 μm are diploid. The other half of section *Pelargonium* encompasses tetraploid, hexaploid, and octoploid species (Fig. 1).

The chromosome numbers correlate well with the proposed sectional classification. The diploid species have a relatively small distributional range in the Cape Province of South Africa; the highest concentration is found in the southwest Cape region (Albers & van der Walt, 1984). The high polyploids, *Pelargonium capitatum*, *P. graveolens*, and *P. radens*, are much more widespread in distribution; *P. graveolens*, for example, extends from the eastern Cape to Zimbabwe.

In section *Ligularia*, chromosomes of the larger size occur exclusively. The 27 species are considered to be advanced. They are woody or herbaceous subshrubs, sometimes with semisucculent stems. In this section the basic chromosome number $x = 11$ is also found, but the chromosomes are double the size of those of section *Pelargonium*. The DNA content of a 22-genome of the large type corresponds well with that of the high polyploid genome of the smaller size.

Other numbers in section *Ligularia* are $2n = 20$ (two species), 18, and 16 (Fig. 1). With $x = 11$ basic in the section, these numbers constitute a decreasing aneuploid series (Albers, 1984). There are also a few tetraploids based on $n = 9$ and 8. *Pelargonium grandicalcaratum* with $2n = 58$ is probably an amphiploid species evolved from a diploid (22) and a tetraploid (36) species (Fig. 1).

Though section *Ligularia* has a wide distribution throughout the region of southern Africa, the diploid species with $2n = 22$ occur in a limited area of the west coast where winter rainfall conditions prevail. Most of the diploid species with $2n = 18$ and 16 occur along the southern coast, where they receive summer and winter rainfall, but a few are found in the summer rainfall region of the eastern Karoo and in the Kalahari Highveld transition zone of Transvaal, Botswana, and Namibia.

Several species in section *Ligularia* with the

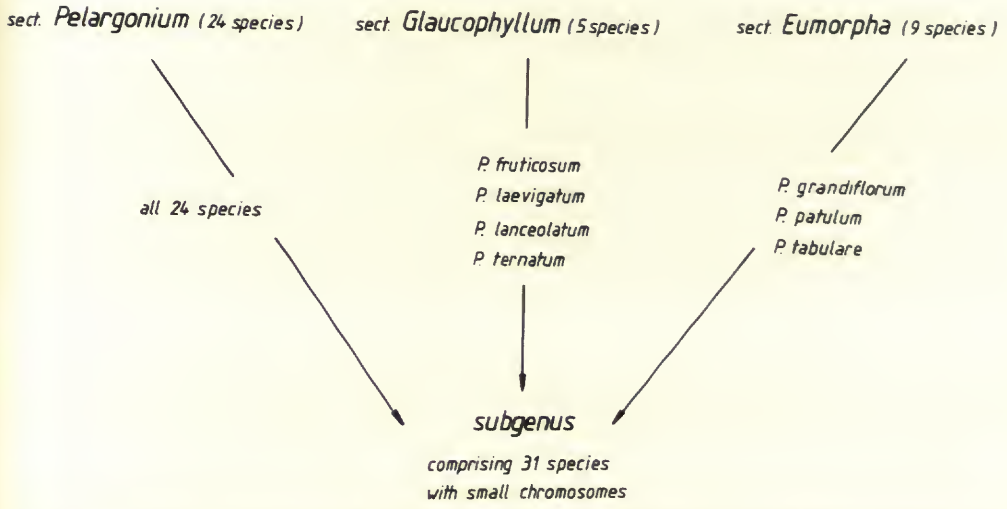

FIGURE 2. Proposed natural grouping of all species with small chromosomes in one subgenus of *Pelargonium*.

same basic number are already considered closely related by morphology. They form natural subdivisions in the section:

$x = 11$	*P. oreophilum, P. hirtum, P. stipulaceum, P. pulchellum*
$x = 9$	*P. griseum, P. dolomiticum, P. ramosissimum*
$x = 8$	*P. exstipulaceum, P. abrotanifolium*

The occurrence of the basic number $x = 11$ in several sections and in the closely related genera *Monsonia* and *Sarcocaulon* also supports the proposition that this is the basic number for *Pelargonium* (Albers & van der Walt, 1984).

The species with small chromosomes are considered to have the most primitive characters; their basic number is $x = 11$. Most occur with a high concentration in the southwestern Cape Province under relatively moist conditions. The species with the larger chromosomes are much more advanced anatomically and ecologically, having evolved from species with smaller chromosomes. It is evident that another direction in chromosome evolution took place after this new diploid status was achieved. An agreement exists between the distribution areas of the large and small karyotypes with the same diploid chromosome number $2n = 22$.

A similar aneuploid decrease in Geraniaceae is proposed by Yeo (1984) for *Geranium*, and chromosomes of different sizes are known in this genus also (Albers, unpubl.).

It is still uncertain whether the diploid number $2n = 20$ belongs to the decreasing series. This number occurs in one species of *Ligularia*, whereas $2n = 22$ and $2n = 18$ are quite common. Thus we need to consider a possible hybrid origin. The compatibility of the potential parent genomes is well documented in *Pelargonium grandicalcaratum* ($2 \times 18 + 22$). The 20-genome may have evolved twice or more, because species of quite different morphological strategies [stem succulents (section *Ligularia*) and geophytes (section *Hoarea*)] and different distributions contain this number.

One species with $2n = 20$ is *Pelargonium otaviense* (section *Ligularia*); another is *P. spinosum* (section *Glaucophyllum*). Van der Walt & Vorster (1981) consider the latter unique, and only provisionally included it in this section (Van der Walt & Vorster, 1983). All other species in section *Glaucophyllum* have small chromosomes and the diploid number $2n = 22$. In addition to the chromosome number, some morphological characters and the geographic distribution also suggest a closer relationship between *P. spinosum* and *P. otaviense*.

Some of the classical sections cannot be upheld from a karyological point of view and must be replaced by natural groupings such as the proposed subgenus with exclusive species with small chromosomes (Fig. 2).

The origin of the karyotype with $2n = 8$ in *Pelargonium elongatum* is still unknown (Gibby & Westfold, 1983). This can only be a derived number; $x = 4$ is a secondary basic number. The

occurrence of a cultivar with $2n = 9$ described by Daker (1967) as a true haploid may indicate a possible explanation.

The study has shown that chromosome number and chromosome morphology are important phylogenetic considerations in *Pelargonium*. Polyploidy and aneuploidy are evolutionary processes whose directions are readily established and, together with other studies, will contribute to an insight into the interrelationships of the species in the genus *Pelargonium*.

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CLASSIFICATION OF THE ACANTHACEAE: A SOUTHERN AFRICAN PERSPECTIVE[1]

K. Balkwill[2] and F. Getliffe Norris[3]

Abstract

Revision of southern African species of acanthaceous genera has stimulated reappraisals of tribal and subtribal limits within the family. The major classifications of Lindau (1895) and Bremekamp (1965) are reviewed and the potential taxonomic value of the inflorescence, floral characteristics, and pollen morphology are evaluated. A terminal thyrse, the basic form of the inflorescence, appears to be retained in the Acanthinae and Odontoneminae but is much modified in many genera of Justiciinae. At the generic and specific level this character is extremely useful in the latter subtribe. The presence of a rugula in the corolla of *Justicia* and associated genera is distinctive but is absent from a group which includes *Dicliptera*. Our proposal to reinstate Lindau's Diclipterinae is partly based on this. Similarly, the presence of a rugula in *Lepidagathis* suggests that it may be incorrectly linked with *Neuracanthus* in the Lepidagathidae. The nature of the nectariferous disc and morphology of the fruit is also taxonomically useful. The distribution of genera possessing elastic placentae will be discussed. Seed characters including the type of indumentum are valuable. Pollen morphology, the basis of Lindau's classification, is discussed. On the basis of surveys of these and other characteristics in southern African genera, we propose modifications to the existing tribal limits and present an alternative classification.

Résumé

Une révision des espèces du genre Acanthacées dans le sud de l'Afrique a entrainé des réévaluations des limites tribales et sous-tribales dans la famille. Les auteurs examinent les classifications importantes de Lindau (1895) et Bremekamp (1965) et évaluent la valeur taxonomique potentielle de l'inflorescence, des caractères floraux et de la morphologie pollénique. Un thyrse terminal, forme de base de l'inflorescence, semble être retenu dans les Acanthinae et les Odontoneminae mais est tres modifié chez de nombreux genres de Justiciinae. Au niveau générique et spécifique cette caractéristique est extrêmement importante dans cette derniere sous-tribu. La présence d'une rugule dans la corolle de *Justicia* et des genres associés est caractéristique, mais est absente d'un groupe qui comprend *Dicliptera*. Notre proposition d'accepter les Diclipterinae de Lindau est en partie basée sur ce fait. De même, la présence d'une rugule dans *Lepidagathis* suggère que ce genre est peut-être incorrectement relié à *Neuracanthus* dans les Lepidagathidae. La nature du disque nectarifère et la morphologie du fruit sont aussi utiles d'un point de vue taxonomique. La répartition des genres qui ont un placenta élastique est également discutée. Les charactéristiques des graines y compris les sortes de poils sont utiles. Les auteurs parlerent aussi de la morphologie pollinique dui est la base de la classification de Lindau. En se basant sur des études de ces caractéristiques aussi que sur d'autres traits des genres du sud de l'Afrique, nous pensons que des modifications des limites tribales actuelles sont nécessaires et présentons une classification nouvelle.

The Acanthaceae is an interesting and variable family and since 1789, when de Jussieu subdivided it on the basis of two or four stamens, the infrafamilial classification has received attention from many authors. One of the most significant treatments of this problem is that of Lindau, published in 1895, as he dealt with the family on a worldwide basis. Lindau recognized four subfamilies variously divided into tribes and subtribes. Aestivation was the crucial feature diagnosing the subdivisions of his Acanthoideae, and pollen morphology played an important role in lower ranks. Table 1 summarizes this classification, and southern African genera are placed in their appropriate groups. Burkill & Clarke (1900) and Clarke (1901) contributed significantly to the classification of the African Acanthaceae. Important characteristics were the number of anthers and anther thecae, but pollen characters were not as emphasized as in Lindau's treatment (Table 2). In 1965 Bremekamp published a major work on the reclassification of the family based mainly on his experience of the Asian members. In this he made important modifications by transferring genera previously in the Nelsonioideae sensu Lindau (Nelsonieae sensu

[1] We are grateful to the curators of J, NU, PRE, and K for the loan of material; to the FRD (CSIR) and the University of Natal for research funds; to the Electron Microscope Unit, University of Natal, for technical assistance; and to Dr. Bertel Hansen for his discussion and opinions on this topic.

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TABLE 1. Southern African genera of the Acanthaceae in the context of Lindau's (1895) classification.

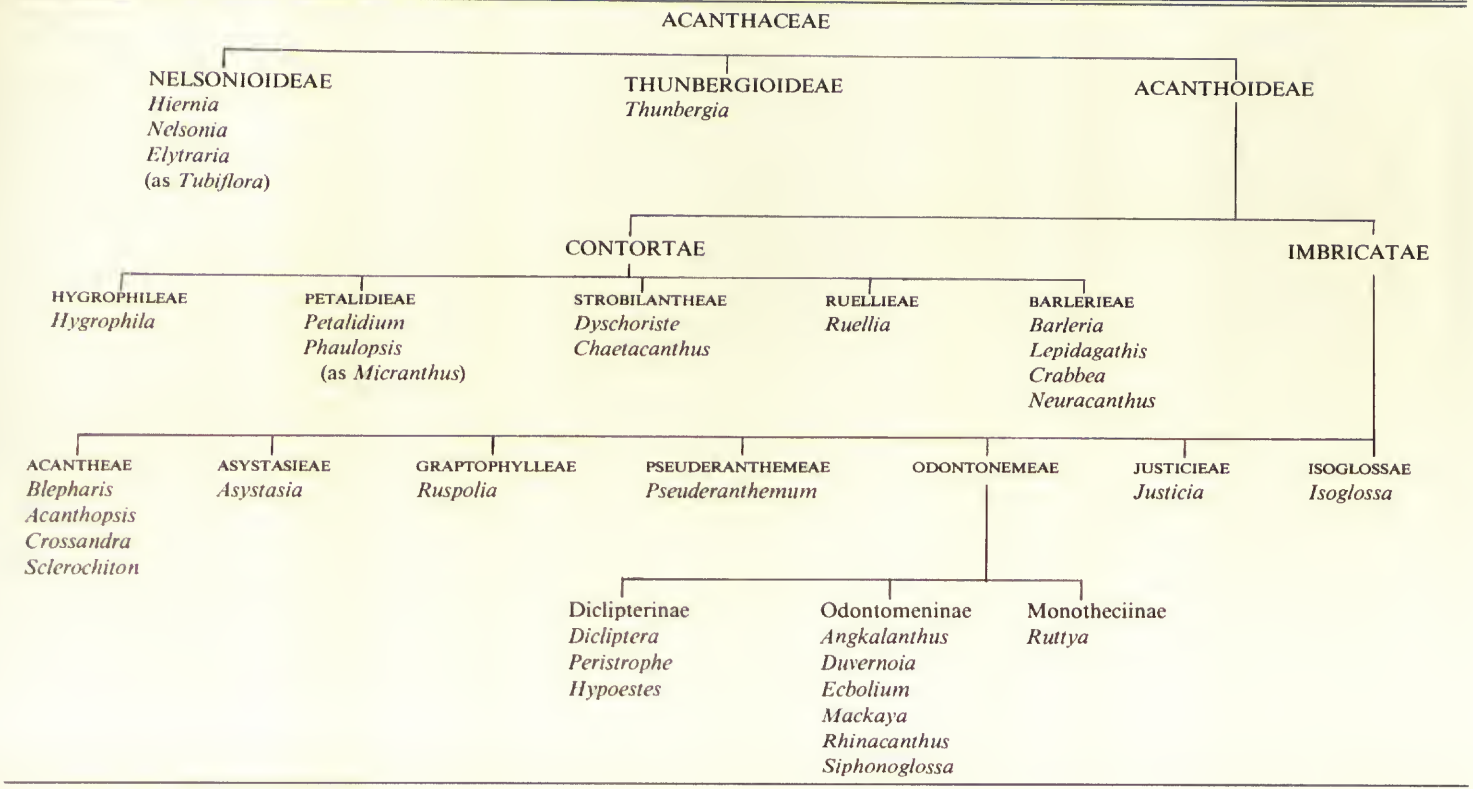
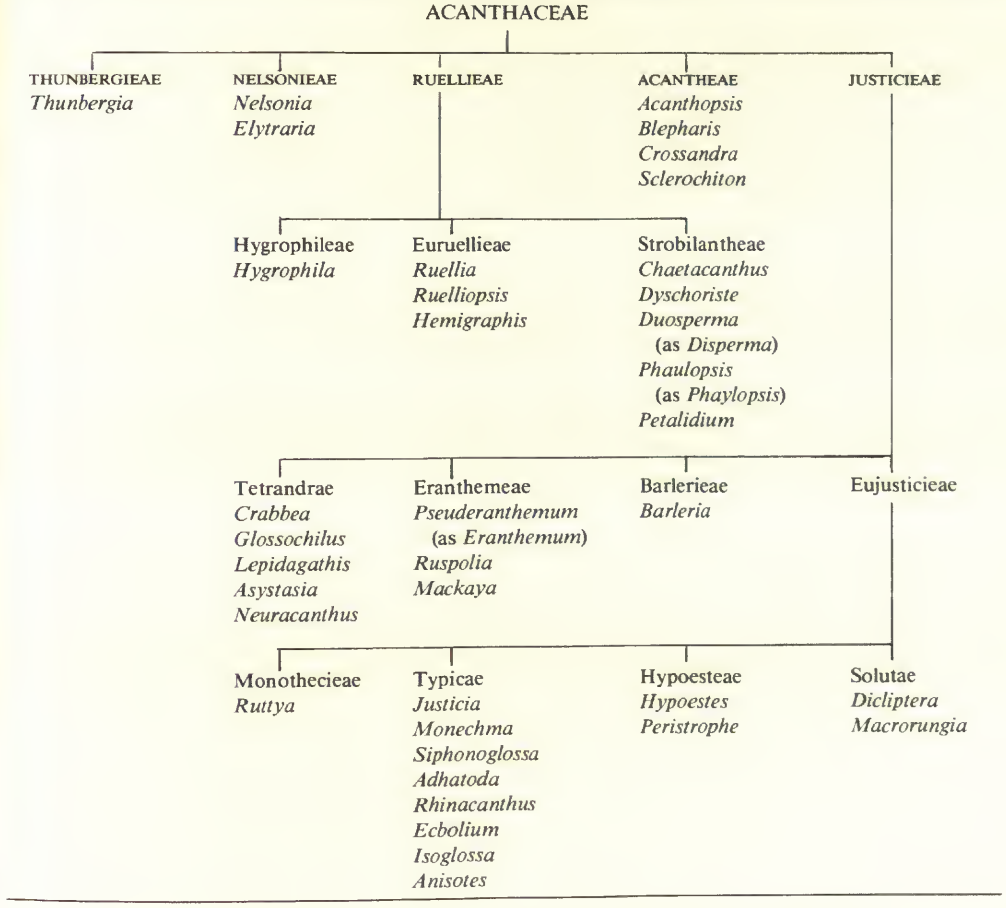


TABLE 2. Southern African genera of the Acanthaceae in the context of the classification used by Burkill & Clarke (1900) and Clarke (1901).

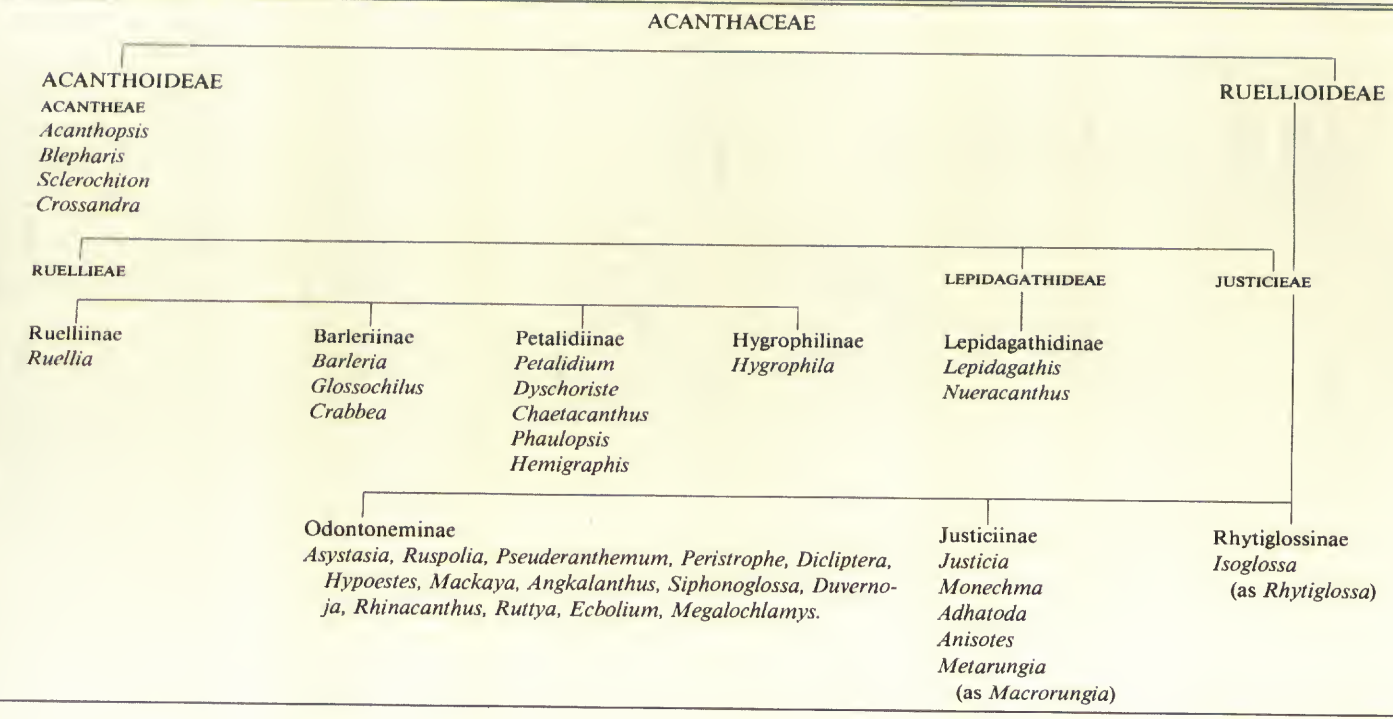


Burkill & Clarke) to Scrophulariaceae and by elevating the Thunbergioideae sensu Lindau (Thunbergieae sensu Burkill & Clarke) to the rank of family. The remaining genera of Lindau's Acanthoideae were reassorted into two subfamilies in the narrowly circumscribed Acanthaceae. By extrapolating from Bremekamp's comments, we have inserted southern African genera into a summary of his classification (Table 3), but in doing so, we have found some anomalies in the southern African material. We suggest that a reappraisal of the infrafamilial groups is necessary. The aim of this paper is to expose these anomalies for further consideration. For the purposes of this discussion of the taxonomic importance of characters we use nomenclature sensu Bremekamp (1965).

METHODS AND MATERIALS

The observations on which our decisions are based were made on herbarium material (from J, K, NU, PRE), living material collected on extensive field trips, and cultivated material grown at the University of Natal, together with spirit-preserved material gathered on field trips. In some instances (e.g., *Peristrophe* Nees, *Dicliptera* Juss., and *Hypoestes* Soland. ex R. Br.) the number of individuals examined is considerable; in others (e.g., *Glossochilus* Nees and *Acanthopsis* Harv.) only a few gatherings were available. Pollen from fresh material or from our recently pressed collections was either cleaned in glacial acetic acid and rinsed in water before mounting on stubs or was placed onto double-sided tape mounted on stubs. Preparations were then dried overnight in

TABLE 3. Southern African genera in the context of the classification of the Acanthaceae proposed by Bremekamp (1965).



a desiccator, coated with gold palladium with a Polaron E5100 sputter coater, and examined with a Jeol JSM T200 or a Hitachi S570 scanning electron microscope.

Features Examined

INFLORESCENCE

The most primitive inflorescence in the Acanthaceae is a dichasial cyme (Baden, 1981), and many inflorescence types have evolved from this either by elaboration and subsequent simplification or possibly by direct reduction from the original cyme. One of the most primitive inflorescence forms in the family is a thyrse, and this is retained in some of the southern African genera. A terminal thyrse is characteristic of the southern African Acanthoideae and, in the Ruellioideae, is found in almost all members of the subtribe Odontoneminae. It also occurs in a few genera scattered in other subtribes where it appears to be a relic of the simplest inflorescence state. Features of the inflorescence have been valuable in discussions on the relationships of *Hypoestes* and its allies, which we discuss below, and are important in our discussions of the status of African gatherings of *Neuracanthus* Nees.

COROLLA

The corolla of the southern African members of Acanthoideae is slit along the adaxial suture, but no member of Ruellioideae shares this feature. In Ruellioideae, actinomorphic flowers appear to be simple and the bilabiate forms derived. Contorted aestivation is usually correlated with actinomorphy, thus suggesting that this too is primitive. In subtribe Barleriinae, Bremekamp (1965) drew attention to the diagnostic quincuncial aestivation. Thus aestivation becomes important in assessing relationships within the tribe Ruellieae and is relevant to our discussion of genera such as *Crabbea* Harv., *Lepidagathis* Willd., and *Neuracanthus*. In the zygomorphic members of Ruellioideae, imbricate aestivation is the norm, but patterns of overlap also provide valuable diagnostic features. Another particularly interesting feature of these genera is the restricted distribution of a rugula—a fold in the adaxial lip forming a channel in which the style and stigma is held and shielded from self-pollination. A slightly less specialized means of achieving this separation is seen in the genera in which the filaments restrain the style. This distinction is important in separating subtribes of Justicieae.

DISC

The disc is a body of nectariferous tissue situated at the base of the ovary. It may be annular, saucer-shaped or cupular. A study of vasculature (De, 1967) has shown that in most cases the disc has staminal traces, suggesting that it is derived from the base of the now epipetalous filaments. In some species there is a protrusion that may represent a fifth stamen while many species have awns on the upper surfaces of these discs. In certain populations of *Hypoestes forskaolii* (Vahl) R. Br., the awns look remarkably like staminodes (pers. obs.). In Acanthoideae, Lepidagathideae, and most of Ruellieae, the disc is annular, while in most members of Justicieae it is cupular. Most of the discs of the species of the Justiciinae that have been investigated have awns.

ANDROECIUM

Many features of the androecium provide important diagnostic features. These include number of stamens, presence of staminodes, relative lengths of filaments, degree of fusion of filaments, and details of the anther including the number and disposition of thecae and their appendages.

All Acanthoideae have four stamens, but in Ruellioideae four, two, or even five occur and may or may not be combined with staminodes. In *Barleria* it is a particularly important feature, as all permutations of stamens with or without staminodes are recorded and the size of the stamens may vary markedly. Didynamous stamens are common in the subfamily and in several genera the filaments are united into a flap or flange of tissue decurrent on the corolla tube. The distal edge of this tissue bears individual short stamens and staminodes. This peculiar arrangement has been important in assessing the positions of *Chaetacanthus* Nees, *Hygrophila* R. Br., and *Hemigraphis* Nees, as we will discuss below. The number of thecae appears to be useful at the generic level. *Hypoestes,* which has monothecous anthers, is closely allied to *Dicliptera* and *Peristrophe,* both of which have bithecous anthers. A very peculiar dimorphism in the anthers of *Neuracanthus* and some African *Lepidagathis* is the existence of both monothecous and bithecous anthers in one flower. The relative position of the thecae appears to be a subtribal feature, parallel thecae characterizing Odontoneminae and

FIGURE 1. Dehisced capsules of various acanthaceous genera: with elastic placental bases (a–e), with inelastic placental bases (f–k), without a stalk (i), with a stalk (j) with four retinacula, two from each locule (k). From the following specimens: *Petalidium variabile* (Engl.) C. B. Clarke, *Craven s.n.* (a); *Phaulopsis longifolia* T. Thoms., *Bourquin s.n.* sub *NU 32938* (b); *Dicliptera heterostegia* Nees, *Balkwill 174* (c); *Dicliptera clinopodia* Nees,

superposed thecae more common in Justiciinae. Appendages such as tails, spikes, or cilia on anthers are common and, as they could hook onto the bodies of visitors thus shaking pollen out of the anthers, are probably of considerable biological importance.

FRUIT

Two features of the fruit provide useful characters at the tribal level—presence or absence of a stalk and the method of dehiscence. Stipitate capsules (Fig. 1j) are found only in Justicieae, while all other acanthaceous capsules are sessile (Fig. 1i). The distinction between capsules with elastic placentae (Fig. 1a–e) and those with inelastic placentae (Fig. 1f–k) has been used frequently in attempts to explain relationships between genera and will be discussed in connection with the subtribes within Justicieae. The number of seeds in the capsule is a generic marker in many instances and may be significant in discussions of the true position of *Hemigraphis* and *Hygrophila,* which differ from the Petalidiinae by having more than two seeds in a locule (Fig. 1k).

SEEDS

A range of hair types associated with the seeds has proven important. Some genera of Acanthoideae and all Justicieae lack hygroscopic hairs and in the latter, seed coat texture and the presence of tubercles on the seeds provide characters that are diagnostic at the subtribal, generic, and specific levels.

PALYNOLOGY

Pollen morphology has long been recognized as an important feature. Indeed, Lindau (1895) relied very heavily on this feature in his classification. More comprehensive surveys have often revealed gaps in Lindau's information (Immelman, 1983), and Burkill & Clarke (1900) were particularly critical of the absolute reliance on pollen features as generic markers. Nevertheless, there appear to be common patterns within tribes against which aberrant genera can be contrasted. This is true of assessments of the positions of *Crossandra* Salisb. and of material assigned to *Neuracanthus.* Features that are emphasized are the shape of the grain, the nature of the apertures, the texture of the exine, and the presence or absence of a margocolpus. The Acanthoideae have colpoid pollen grains (Fig. 2a, d), but of a different shape in *Crossandra* (Fig. 2d). Ruellioideae have colporate or porate grains. Ruelliinae and Barleriinae have spheroidal porate grains (Fig. 2b, e, f). Petalidiinae sensu Bremkamp have prolate grains with bordered pores in bands of solid exine (Fig. 2g, h). Justicieae are characterized by colporate grains with pseudocolpi (colpoid streaks sensu Raj, 1961; Balkwill & Getliffe Norris, 1985) (Fig. 3c–h). A range of pollen morph types occurs in Justicieae. Prolate tricolporate grains with undissected margocolpi are probably the primitive state (Fig. 3f), and derived forms show progressive dissection of the margocolpi into areoli (Fig. 3g) and reduction in number of colpi from three to two (Fig. 3h). *Isoglossa* Oerst. has spheroidal grains unlike those of any other southern African genus in the family (Fig. 3i), with two polar pores, a girdle of pusticulate exine around the equatorial circumference, and a spinescent surface.

Aspects of these features have been considered in a survey of southern African members of the Acanthaceae and have helped to shape our ideas on the tribal limits.

Discussion

Our discussion of southern African genera in the Acanthaceae is based on a concept of the family that excludes both Thunbergioideae and Nelsonioideae sensu Lindau. The former was raised to familial rank by Bremekamp (1953, 1965)—a decision that has general acceptance. His recommendation that Nelsonioideae be assigned to the Scrophulariaceae has met with opposition from specialists in Acanthaceae taxonomy (Johri & Singh, 1959; Reddy et al., 1980) and from those studying Scrophulariaceae (Burtt, 1965). At least one author has raised Nelsonioi-

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Balkwill 213 (d); *Metarungia galpinii* (Baden) Baden, *Batten* sub *Balkwill 1725* (e); *Peristrophe cernua* Nees, *Balkwill 450* (f, j); *P. grandibracteata* Lindau sensu lato, *de Winter & Leistner 5828* (g); *Anisotes rogersii* S. Moore, *Strey 3497* (h); *Ruelliopsis setosa* C. B. Clarke, *Balkwill 1656* (i); and *Ruellia patula* Jacq. sensu lato, *Balkwill & Manning 628* (k). Scale line = 1 cm.

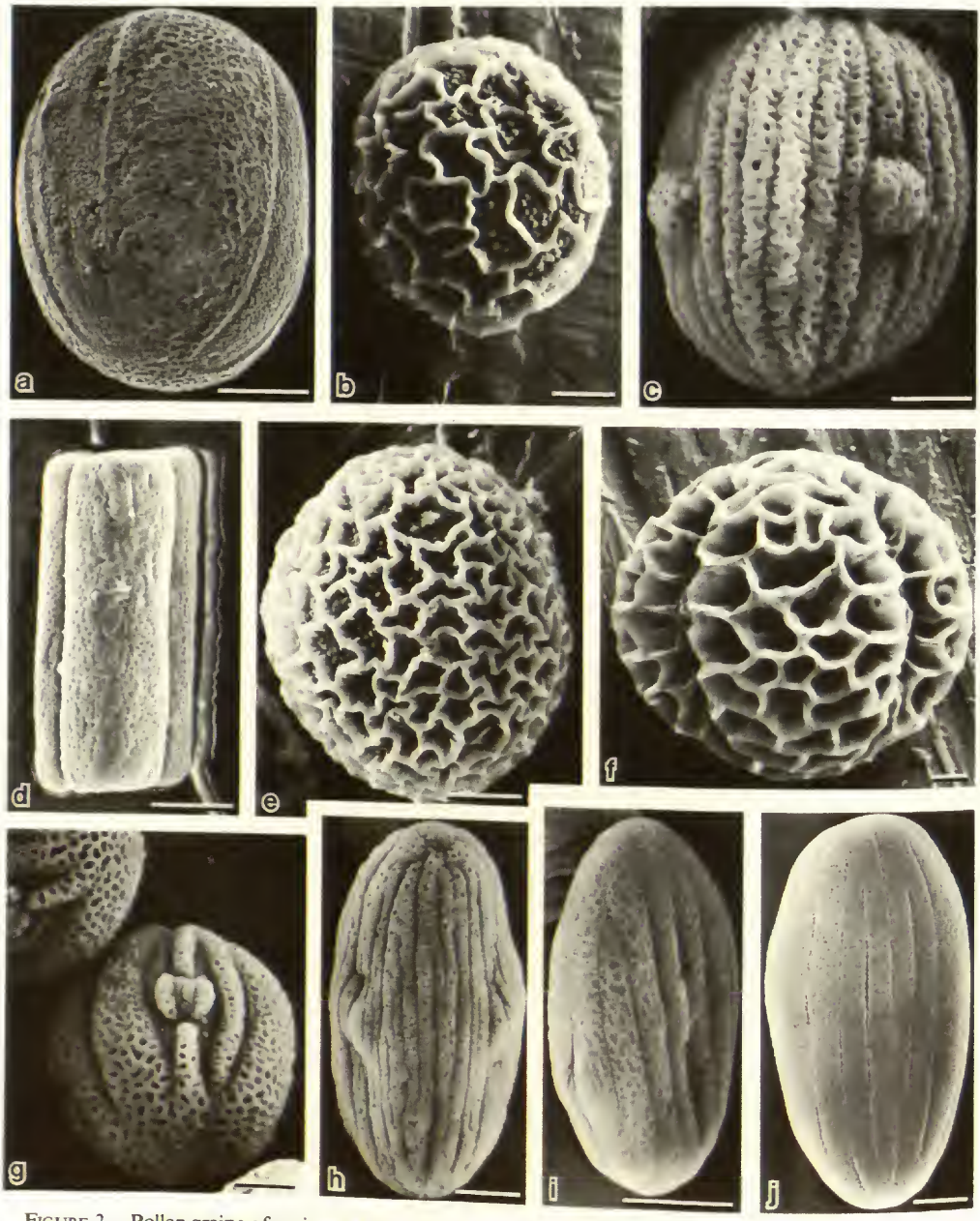

FIGURE 2. Pollen grains of various acanthaceous genera.—a. *Acanthopsis disperma* Nees, *Kerfoot 6333.*—b. *Crabbea hirsuta* Harv., ex hort. Botanical Garden, Univ. of Natal.—c. *Ruelliopsis setosa* C. B. Clarke, *Balkwill 1656.*—d. *Crossandra spinosa* Beck, *Kerfoot 7370.*—e. *Ruellia* sp., *Balkwill & Manning 690.*—f. *Barleria spathulata* N. E. Br., *Balkwill & Manning 675.*—g. *Petalidium oblongifolium* C. B. Clarke, *Balkwill 1573.*—h. *Chaetacanthus* sp. nov., *Balkwill & Edwards 1406.*—i. *Hygrophila auriculata* (Schumach.) Heine, *Balkwill et al. 2946.*—j. *Hemigraphis prunelloides* S. Moore, *Pienaar & Vahrmeijer 490.* Scale lines = 10 μm.

deae to familial rank (Sreemadhavan, 1977). We do not feel competent to comment on these decisions without a far more comprehensive knowledge of Acanthaceae outside southern Africa and of Scrophulariaceae. Bremekamp (1965) accepted two subfamilies within his narrow view of the Acanthaceae, Acanthoideae, and Ruellioideae. This appears to be a logical subdivision,

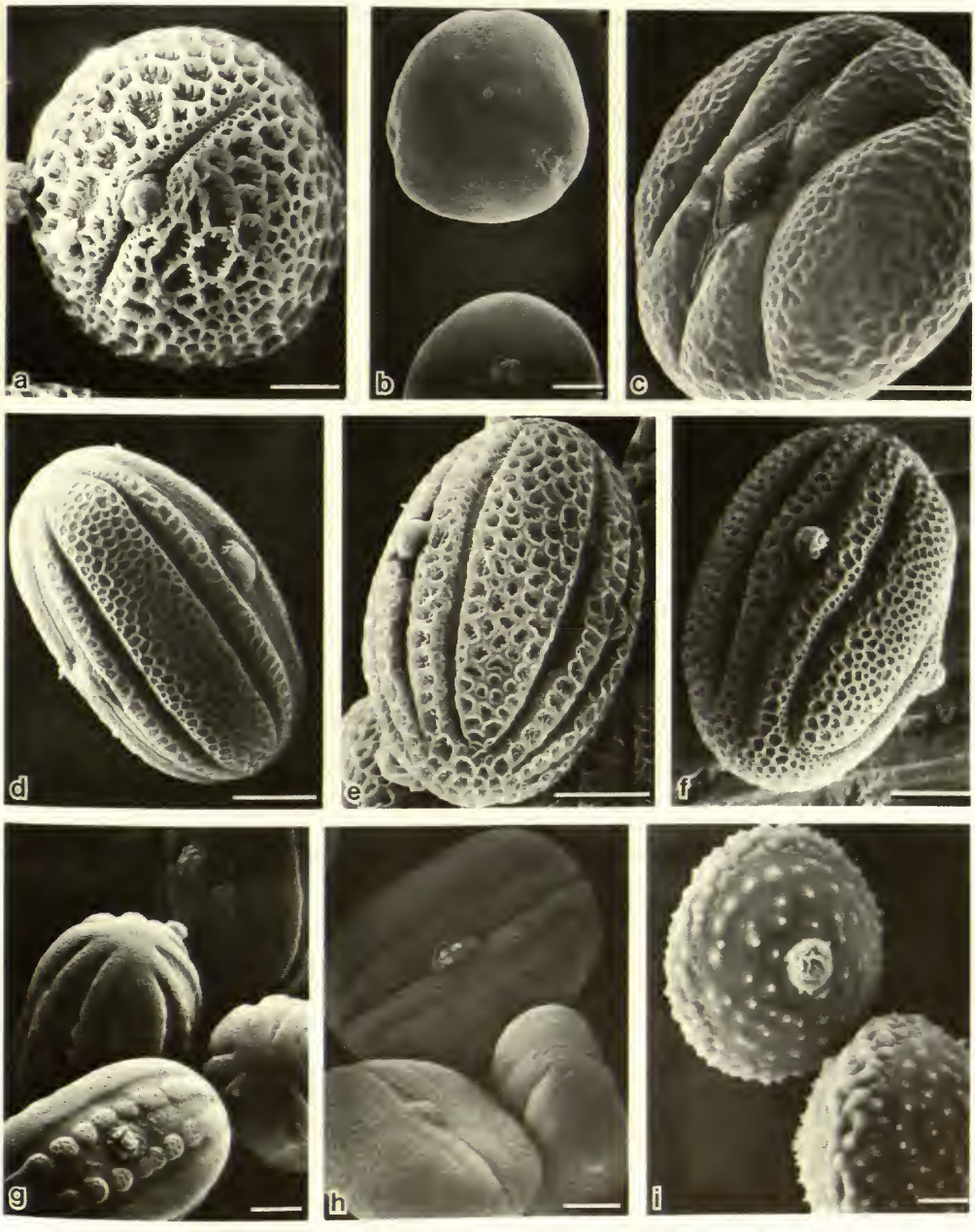

FIGURE 3. Pollen grains of various acanthaceous genera.—a. *Lepidagathis scabra* C. B. Clarke, *Jacobsen 2391.*—b. *Neuracanthus africana* [T. Anders. ex] S. Moore, *Balkwill 1620.*—c. *Glossochilus burchellii* C. B. Clarke, *Leistner 1397.*—d. *Dicliptera* sp. nov., *Balkwill 1574.*—e. *Periestes* sp., *Baron 6138.*—f. *Rhinacanthus gracilis* Klotzsch, *Balkwill 471.*—g. *Anisotes rogersii* S. Moore, *Balkwill 1622.*—h. *Duvernoia aconitiflora* A. Meeuse, *Balkwill 1518.*—i. *Isoglossa hypoestiflora* Lindau, *Balkwill 344.* Scale line = 10 μm.

but at the tribal level we find anomalies. Lindau, Burkill & Clarke, and Bremekamp all regard the genera *Blepharis* Juss., *Acanthopsis, Sclerochiton* Harv., and *Crossandra* as a discrete tribe. Lindau, because of his fundamental division on the basis of corolla aestivation, places this tribe in the Imbricatae, where it has equivalent status to and relatively close affinity with Justicieae. Bre-

mekamp, however, places it in Acantheae, and the array of characters unique to this tribe supports Bremekamp's decision. These characters are the one-lipped corolla, four monothecous ciliate anthers, and colpate pollen, which we believe are far more significant than the aestivation. The inclusion of *Crossandra* with the other southern African genera, however, is debatable. *Crossandra* differs from the others, as the corolla is in the red and yellow range, not in the range of white, blue, and purple; the corolla tube is proportionally much longer; the filaments are small and ephemeral, not hard and chitinous; the anthers and stigma are included in the tube and not exserted; the pollen grains have squared ends, not rounded ones; and the surface of the pollen grains is foveolate, not shallowly reticulate (Fig. 2d). *Crossandra* is therefore anomalous in the Acantheae, but bears closer relationship to this tribe than to any other in the subfamily. We believe it may be justified to place *Crossandra* in a subtribe of its own within Acantheae.

Ruellieae sensu Bremekamp is subdivided into three subtribes: Ruelliinae, having globose reticulate pollen with three to seven evenly spaced pores and actinomorphic or subactinomorphic corollas with contorted aestivation; Barleriinae, with similar pollen, zygomorphic flowers, and quincuncial or opposite aestivation; and Petalidiinae, having prolate banded pollen with pores surrounded by lips of margocolpus, bilabiate, or subactinomorphic flowers borne in axillary cymes, and with didynamous stamens often attached to a flap of tissue decurrent on the corolla tube.

Ruelliopsis C. B. Cl. has banded pollen grains with lips of margocolpi surrounding the pores (Fig. 2c), a form that is rather different from that of *Ruellia* (Fig. 2e), but on the basis of the corolla form and the number of seeds in each locule, we feel it must be retained in the Ruelliinae.

The genus *Crabbea* was placed in Barleriinae by Bremekamp on the basis of its similar aestivation, but our observations reveal that in *Crabbea* the two inner petals are opposed, not adjacent to one another. *Crabbea* also has didynamous stamens (not a feature of other members of the Barleriinae) and pollen almost identical to that of *Ruellia* L. (cf. Fig. 2b, e). We therefore propose that *Crabbea* be placed in the Ruelliinae.

Glossochilus is a second genus of Barleriinae that appears incorrectly placed. It has colporate pollen (Fig. 3c) and didynamous stamens, which do not fit into the definition of Ruellieae at all, but rather fit more comfortably with the subtribe Odontoneminae, where its aestivation and corolla shape suggest close affinity with *Asystasia* Blume. *Glossochilus* is unusual in that subtribe, as it does not possess a terminal thyrse, and this may account for its former position in Barleriinae; but this dissimilarity is overridden by the many features it has in common with *Asystasia.*

Removing *Glossochilus* and *Crabbea* from Barleriinae leaves *Barleria* L., a genus that shows a great deal of variation in number of stamens and staminodes, number of ovules, shape of fruit and inflorescence type. This degree of variability is far higher than that displayed in many genera, especially those in Justicieae (pers. obs.; Hansen, pers. comm.), and revision of the genus is evidently necessary.

The Petalidiinae, the third subtribe in the Ruellieae, is the largest. *Duosperma* Dayton (which Clarke described as *Disperma* C. B. Cl., in the tribe Strobilantheae senus Lindau) presumably would be placed in the subtribe Petalidiinae by Bremekamp. Similarly, *Dyschoriste* Nees and *Chaetacanthus* with axillary cymes have been removed from Strobilantheae to Petalidiinae. These genera share unusual pollen morphology. The grains are ellipsoidal, with pusticulate exine divided into narrow longitudinal bands (Fig. 2h). *Chaetacanthus,* despite its two stamens, fits neatly into this subtribe of the Ruelliae and appears to be a more derived form.

Hemigraphis poses many problems at generic and tribal levels. Nees described two very different species at the time he described the genus. Neither has been designated as a type (Farr et al., 1979). Since 1847, a number of other species have been described, and Hansen (pers. comm.) has indicated that the Asian species in this genus are considered by Terao to be *Strobilanthes* species and that much of the African material has been misidentified. Heine (1971) transferred many of the African species of *Hemigraphis* to *Hygrophila.* During the course of our study, however, it has become evident that southern African material identified as *Hemigraphis prunelloides* S. Moore cannot be congeneric with our *Hygrophila* species. The former has small actinomorphic flowers that lack a rugula, while *Hygrophila auriculata* (Schumach.) Heine and *H. gracillima* (Schinz) Burkill, the two species we have seen, have distinctly bilabiate corollas with distinct rugulae in their upper lips. Pollen morphology (Fig. 2i, j) and ovule number are, however, very similar. It appears that a very careful

revision of *Hygrophila* and *Hemigraphis* including a thorough survey of floral morphology is required. Bremekamp placed *Hemigraphis* in the subtribe Petalidiinae (with *Dyschoriste* and *Chaetacanthus*) and segregated *Hygrophila* in its own subtribe, Hygrophilinae. We believe this overlooks the close relationship between *Hygrophila* and *Hemigraphis* and also the unusual staminal arrangement common to these two genera, *Dyschoriste, Chaetacanthus,* and other genera in the Petalidiinae. In all these genera, stamens (and staminodes in *Chaetacanthus*) are attached to the top of a flange of tissue that is decurrent on the corolla tube in a manner reminiscent of *Strobilanthes*. We wonder if it would not be more appropriate to include *Hygrophila* in the subtribe Petalidiinae.

Similarly we observed that *Lepidagathis scabra* C. B. Clarke resembles *Hygrophila* in corolla shape, rugula, and colporate pollen (Fig. 3a). Thus it may not be justified to separate *Lepidagathis* as Bremekamp suggested, but to assign it to the subtribe Petalidiinae. Some of the African species of *Lepidagathis* have monothecous posticous anthers and, as the number of thecae in the posticous anthers appears to be the only feature used to separate *Lepidagathis* and *Hulemacanthus* S. Moore, a reappraisal of the generic limits is indicated. If this distinction is valid, then new combinations must be made. Southern African herbaria include gatherings named *Neuracanthus*. While the Asian species of *Neuracanthus* are bilabiate, as is the type species *N. tetragonostachys* Nees, the African species referred to this genus are quite different. The corolla is tubular below, rotate above, the lobes are barely separated and are induplicate in the bud. Features of this plant that are unique in the southern African Acanthaceae include this corolla form; the globose, tricolporate pollen with very small pores in the exine (Fig. 3b); the two-lobed calyx; and the developed dorsal stigma lobe. Inclusion of the sexual parts in the narrow corolla tube is unique in the Ruellioideae, while the axillary thyrse and bifurcated filaments are unique amongst the southern African members of Ruellioideae, excluding the Justicieae. Thus it appears that these plants do not belong to the genus *Neuracanthus* and, furthermore, it is possible that they do not belong in any of the tribes described in the Acanthaceae. Clearly this deserves further attention.

Justicieae is clearly distinguished from all other tribes in the subfamily by the lack of hygroscopic hairs on the seed surface. Three subtribes—Odontoneminae, Rhytiglossinae (syn. Isoglossinae), and Justiciinae—are recognized by Bremekamp. The pollen of *Glossochilus burchellii* Nees, the type species, is almost identical to that of *Asystasia stenosiphon* Clarke, while the corolla is very similar to that of *Asystasia gangetica* sensu lato. The seeds are similar to those of *Asystasia* and, as indicated by Clarke, the only difference between the genera is in the inflorescence. *Asystasia* has a terminal monochasium; *Glossochilus* has individual flowers in leaf axils. Bremekamp has described the species *Glossochilus parviflorus* Hutch. as *Asystasia atriplicifolia,* further emphasizing the fact that these two genera are very closely related and that their interrelationship must be assessed. The very close relationship between *Glossochilus* and *Asystasia* reinforces our recommendation to move *Glossochilus* to the Odontoneminae. Although the four stamens and campanulate corolla of these genera are very unusual in the subtribe, *Mackaya,* which also has a campanulate corolla, has two stamens and thus provides a link with other Odontoneminae, as does *A. stenosiphon* with its bilabiate corolla. These links make it impossible to place *Asystasia* and *Glossochilus* in a separate tribe and suggest that it would be unwise to place them in a separate subtribe. *Angkalanthus* Balf. f. is unusual in Odontoneminae, as it has two stamens and no staminodes, but the parallel anther thecae, the nonresupinate corolla without a rugula, and the tricolporate pollen confirm its affinity with the Odontoneminae.

Peristrophe, Dicliptera, and *Hypoestes* are unique in the Justicieae as they have resupinate corollas of a very similar form. They are bilabiate with lips of about the same length as the corolla tube. The lip, which is in the upper position, is narrowly elliptic and has three small teeth at the tip; the lip in the lower position is usually lanceolate or ovate and is emarginate at the tip. The pollen of these three genera is nearly identical, the only variation being in the configuration of the pseudocolpi, which may be separate (Fig. 2d) or confluent at the poles. All three genera have compound inflorescences composed of monochasial units surrounded by a pair of bracts. In *Hypoestes* these monochasia may be variously reduced (Balkwill & Getliffe Norris, 1985). These three genera have no staminodes and so do not belong in the Odontoneminae. As they have no rugulae in their upper lips (held in the lower position), they do not belong in the Justiciinae. *Periestes,* a genus from Madagascar and the Co-

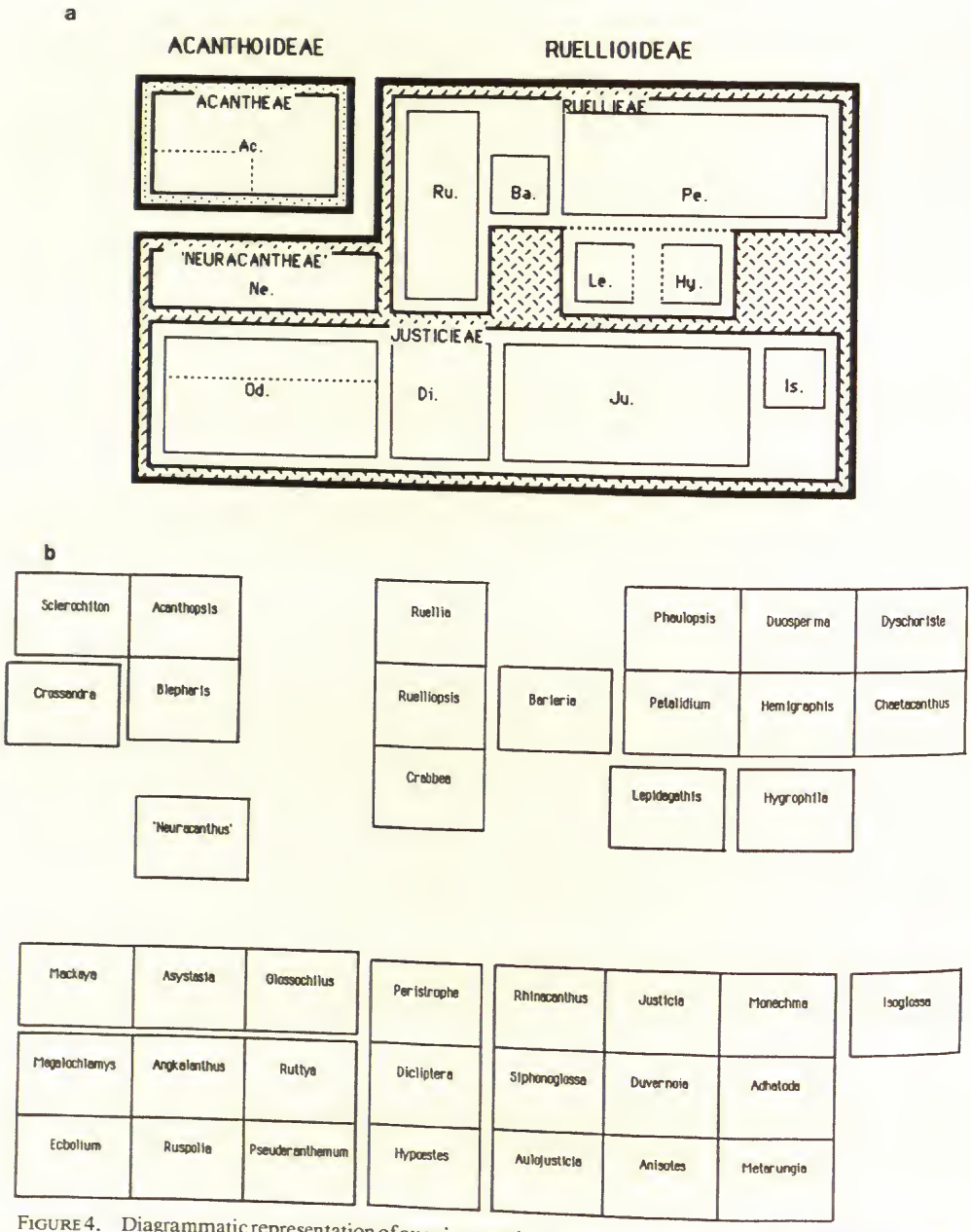

FIGURE 4. Diagrammatic representation of our views on the classification of the southern African Acanthaceae (a) and of the placement of southern African genera (b). Thick lines represent boundaries of subfamilies, medium lines of tribes, thin lines of subtribes, and dotted lines represent boundaries of which we are uncertain. Abbreviations represent subtribes: Acanthinae (Ac.), Ruelliinae (Ru.), Barleriinae (Ba.), Petalidiinae (Pe.), Lepidagathidinae (Le.), Hygrophilinae (Hy.), Odontoneminae (Od.), Diclipterinae (Di.), Justiciinae (Ju.), and Isoglossinae (Is.).

mores, shares all of these characters, including pollen morphology (Fig. 3e), and Lindau placed *Periestes* with *Peristrophe, Dicliptera,* and *Hypoestes* in his tribe Diclipterinae. We propose that Diclipterinae be reinstated, but, as Bremekamp suggested, without *Rungia,* which has a rugula (cf. Justiciinae) and does not have a resupinate corolla. Burkill and Clarke separated

Dicliptera from *Peristrophe* and *Hypoestes,* emphasizing the elastic placental bases in *Dicliptera* (Fig. 1c, d) and *Metarungia* (Macrorungia) (Fig. 1e). Elastic placentae occur in *Rungia* (Justicinae) and in *Petalidium* (Fig. 1a) and *Phaulopsis* (Fig. 1b), two genera of the Petalidiinae. The phenomenon therefore appears to have evolved more than once in the family. We believe that differences in other features override the apparent similarity in the dehiscence of the capsules of *Dicliptera* and *Metarungia.* The capsule of *Dicliptera* is thin-walled and has a raphe to which the elastic placental bases are attached (Fig. 1c, d), while the capsule of *Metarungia* is thick-walled, woody, and without a raphe (Fig. 1e) and has much more in common with the woody capsule of *Anisotes* (Fig. 1h). Thus, Diclipterinae accommodates *Dicliptera, Peristrophe,* and *Hypoestes* and in terms of inflorescence morphology, floral morphology, seed size, seed shape, and seed texture appears to be a more natural group in which we accept differences in capsule dehiscence and number of anther thecae as generic characters. Similarly, *Metarungia* and *Anisotes* form a second natural group with bird-pollination and broad, tubular, red-brown corollas in common. Thus we consider the form of dehiscence to be important at generic level but not necessarily indicative of tribal relationships.

Burkill and Clarke placed *Isoglossa* in the same group as *Justicia,* but Lindau and Bremekamp segregated it on the basis of its extraordinary pollen. We support the latter decision.

With the removal of the Diclipterinae and Isoglossinae, Justiciinae is a more homogenous subtribe, characterized by bilabiate corollas with distinct rugulae in their upper lips, two stamens, and no staminodes. The upper lip is very often hooded. Generic limits within the subtribe are poorly defined or based on single characters. Intensive study in progress at present includes reassessment of *Justicia* (Immelman, 1983), *Duvernoia* and *Adhatoda* (Manning & Getliffe Norris, 1985) and *Monechma* (Munday, 1980). The relationship of *Aulojusticia* and *Siphonoglossa* will also be investigated by Immelman, as Clarke placed *Aulojusticia* in synonymy with *Siphonoglossa,* while Dyer (1975) maintained *Aulojusticia* as a separate genus.

Conclusions

We conclude that the southern African Acanthaceae belong to two subfamilies, the Acanthoideae and Ruellioideae sensu Bremekamp. We find that all the southern African Acanthoideae belong to the tribe Acantheae but suggest that *Crossandra* may deserve to be placed in its own subtribe. The Ruellioideae in southern Africa represent at least two, if not three, tribes. These are Ruellieae, Justicieae, and a tribe as yet undescribed, which will include the African species mistakenly identified as *Neuracanthus.* The Ruellieae comprise at least three subtribes—Ruelliinae, Barleriinae, and Petalidiinae. *Hygrophila* and *Lepidagathis* may represent another two subtribes in Ruellioideae. Within Justicieae there are four subtribes represented in southern Africa, including the Diclipterinae originally described by Lindau, which we suggest must be amended and reinstated. Our views on the subdivision of the family and classification of the southern African genera are presented in Figure 4. During the course of this survey, many intriguing taxonomic problems have been illuminated that confirm our opinions of this as an interesting and challenging family.

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FLORA AND VEGETATION OF THE DAHOMEY GAP—A CONTRIBUTION TO THE PLANT GEOGRAPHY OF WEST TROPICAL AFRICA

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ABSTRACT

Due to the completion of the *Flore Analytique du Togo* (Brunel et al., 1984) and to the recent investigations in Benin and Ghana, our botanical knowledge of this part of tropical West Africa has increased considerably. If we try to interpret those investigations, we may say that the "Dahomey Gap" includes essentially the drier types of the Guineo-Congolian forest belt in southeastern Ghana, southern Togo, and parts of southern Benin (formerly Dahomey). In fact, three rather particular types of drought-resistant forests can be found even today in this part of West Africa: two are confined to the south of latitude 7°N and the third one to the north of this parallel. The two southern forest types are three-layered with taller emergent deciduous trees, an understory of smaller, mostly deciduous trees, and another of essentially evergreen shrubs, treelets, and lianas. The northern type is more or less two-layered with a well-developed herbaceous ground cover under the canopy of rather high trees. The corresponding secondary plant communities are dense, evergreen shrubberies in the south and savannalike woodland interspersed with tall grasses in the north. Possibly savanna trees such as *Daniellia oliveri* or *Prosopis africana* are negatively affected by the effects of a small rainy season occurring south of the 7th parallel. Since forests of the northern type are found on deep soils on even surfaces as far north as 8.5°N, the southern extension of White's mapping unit 27 in his *Vegetation Map of Africa* in Ghana, Togo, and Benin seems to extend too far to the south. Instead, the situation in these northern parts of the Dahomey Gap strongly resembles that of the V-Baoulé, a similar interval of the Guinean forest belt in Ivory Coast, and even more that of northern Nigeria, where White uses his mapping unit 12 for the area around Ilorin.

RÉSUMÉ

Si nous essayons d'interpréter ces études, nous pouvons dire que la discontinuité dahoméenne comprend essentiellement les types plus arides des forêts guinéo-congolaises dans le sud-est du Ghana, le sud du Togo, et des parties dans le sud du Bénin (anciennement Dahomé). En fait, trois types assez particuliers de forêt qui résistent à la sécheresse peuvent se trouver encore aujourd'hui dans ces régions de l'Afrique occidentale: deux sont restreints au sud du 7ème parallèle et le troisième au nord de ce parallèle. Les deux types présentent trois étages: les arbres dominants à feuilles caduques, un étage dominé d'arbres plus petits surtout à feuilles caduques, et un étage composé essentiellement de buissons sempervirents, d'arbrisseaux et de lianes. Le type du nord est plus ou moins fait de deux étages, comprenant une couche herbacée bien developpée sous des arbres assez hauts. Les communautés de plantes secondaires correspondantes sont composées de buissons sempervirents denses dans le sud et de forêts de savane parsemées d'herbes hautes dans le nord. Il est possible que des arbres de savane tels que *Daniellia oliveri* ou *Prosopis africana* soient influencés négativement par une courte saison des pluies qui survient au sud du 7ème parallèle. Comme les forêts de type du nord se trouvent sur des sols profonds en terrain plat au nord jusqu'à 8,5°N, l'extension vers le sud de l'unité cartographique no. 27 de White (*Vegetation Map of Africa*) dans le Ghana, le Togo et le Bénin semble s'étendre trop loin. La situation dans ces régions du nord de la discontinuité dahoméenne ressemble beaucoup à celle du V-Baoulé, une discontinuité semblable dans la ceinture forestière de Guinée sutiée en Côte d'Ivoire, et encore plus à celle du nord du Nigeria où White utilise son unité 12 pour la région autour d'Ilorin.

One of the striking features of West African vegetation is the interruption of the belt of closed tropical rain forest of White's (1979) Guineo-Congolian region on the territories of southeastern Ghana, southern Togo, and most of southern Benin, the former Dahomey. This Dahomey Gap or Dahomey Interval (White, 1979) stretches from Elmina (near Cape Coast, Ghana) to Porto Novo in eastern Benin. Starting as a narrow strip of open country in the west, it widens towards the east, forming first the Accra Plains of southern Ghana, the vegetation of which has been described by Jenik & Hall (1976). North of the delta of the Volta River a small mountain chain

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extends from SSW to NNE, separating Ghana and Togo. These mountains, which attain nearly 1,000 m in the south (Mont Agou in Togo), bear semideciduous forests on the slopes and in the valleys. Due to the very shallow soils, the tops of many of these hills are covered with grassland and trees such as *Lophira lanceolata, Daniellia oliveri, Pericopsis laxiflora,* and other species typical of West African savannas.

Whereas most modern vegetation maps clearly show the well-forested Togo Mountains, the rest of the territory between the mouth of the Volta River and the Nigerian border is either shown to be covered by Guinea-type savannas (Diels et al., 1963) or by a "mosaic of Guinean-Congolian lowland rain forest and secondary grassland" (White, 1983). It is the intention of this communication to show that neither savannas of the "Guinean" type nor "lowland rain forest" vegetation are found in this area and what instead may be or might have been the natural vegetation of the Dahomey Gap.

White (1979) noted that "no published comprehensive account of the vegetation of this well-known and important feature" had so far been published. Since then this situation has not changed much. Together with some more or less local publications mostly concerning southern Benin (Paradis, 1976; Paradis & Houngnon, 1977; Paradis et al., 1978) and the above-mentioned investigations of the Accra Plains, Ern's (1979) and Brunel's (1981) accounts form the basis of this paper. Other important sources are Aubréville (1937) and Hall & Swaine (1981).

Floristically, Ghana, Togo, and Benin are now reasonably well explored (Irvine, 1961; Brunel et al., 1984), even if there still exists no complete list of the plant species of Benin. A short visit to the southern part of this country and to the National Herbarium of Benin at Cotonou (acronym BENIN) in 1983, however, revealed the great similarity of Benin's flora with that of Togo.

The following description of the potential natural vegetation of the area called Dahomey Gap is limited to more or less plain country with normally drained soils, thus excluding the Togo Mountains, the coasts and beaches, the very extensive marshlands, lakes, and lagoons of the coastal plains, and the gallery forests of the watercourses. Starting at sea level, the area rises to about 400 m in the north and is situated between latitudes 6° and 8°N. The climate between 6° and 7°N can be called equatorial: there are two rainy seasons, interrupted by a longer dry season in winter and a shorter one in summer. The northern part between latitudes 7° and 8°N has only one rainy season from March/April to September/October. Annual precipitations are lowest near the coast in the south (700–800 mm/yr.) and may attain 1,200 mm/yr. in the northern section of the area. Geologically the southern part corresponds to the West African Continental Terminal. The northern section is mostly formed by gneissic rocks which can be found as outcrops of various dimensions in many sites.

Quite evidently, the whole area is free from lowland rain forest. (This type of forest appears only in southeastern Benin near the Nigerian border. Two remnants of the once more extensive lowland rain forests of southern Benin—the Forêt de Pobé and the Forêt de Ichédé—are now being studied by P. Houngnon from the Benin National Herbarium. Most of the former rain forests of southern Benin, however, have been converted into oil palm plantations.) On the other hand, there are no real Guinean-type savannas south of latitude 7°N. The more typical trees of those savannas (*Daniellia oliveri, Pericopsis laxiflora,* etc.) only appear, together with the tall savanna grasses, north of latitude 7°N. On coastal sands there exists a very interesting outlier of Guinean-type savanna vegetation in southern Benin: the famous population of *Lophira lanceolata* near Pahou, which has recently been studied by Paradis et al. (1978). The occurrence of this small fragment of savanna on sandy soils near the coast and the more extensive hilltop savannas in the Togo Mountains indicate a close correlation between soils and savanna vegetation in this part of tropical West Africa. On normally drained soils the effect of the double rainy season seems to affect negatively the typical trees of the Guinean savannas such as *Daniellia oliveri, Lophira lanceolata,* or *Piliostigma* (*Bauhinia*) *thonningii.* They seem to be adapted to one prolonged dry season of about five months.

With a closer look at the tree vegetation of the Dahomey Gap, it becomes clear that there are forest patches of varying size scattered all over the area. Aubréville (1937) reported on the very precarious situation of the forests of southern Dahomey and southern Togo. Recent investigations fully support his view.

There are at least three distinguishable forest types to be found in the area, two of them confined to the southern half with its double rainy season and one in the northern part with one rainy season. None of them, however, can be described as a lowland rain forest, since they all lack the main features of true rain forests and

they exist on only 700–1,200 mm rainfall per year. Instead they should be classified as dry semideciduous forests in the sense of Hall & Swaine (1981).

The two southern forest communities correspond more or less to Hall & Swaine's Southern Marginal type and their Inner Zone subtype of dry semideciduous forests. A fine example of a Southern Marginal type forest occurs in southern Togo near Agbata on the southwest shore of Lake Togo. On sandy soils there is a rather extended sacred forest ("Forêt Fétiche") with a peculiar structure. Widely scattered big specimens of *Antiaris toxicaria* subsp. *welwitschii* var. *africana* form the upper layer of the forest, growing up to 25 m and more. A second layer of smaller trees attains 15–20 m and is composed mainly of leguminous trees such as *Albizia zygia, Albizia ferruginea,* and *Millettia thonningii* (perhaps the most typical species of this forest type). A third layer is composed of evergreen shrubs, treelets, and lianas, part of which may remain, after the removal of the tree cover, often described as coastal thicket or coastal scrub. Another variant of degradation of the Southern Marginal type forest arises by the removal of the two lower layers, leaving only the emergent trees amidst big fields. Thus around Cacaveli, near Lomé, we found large specimens of *Antiaris toxicaria* subsp. *welwitschii* var. *africana*—often worshipped by the local population, who tie the girth with a small string—and *Adansonia digitata,* the baobab. Here and there some small trees of *Dialium guineense* or *Albizia glaberrima* also appear between the fields of maize and other crops. *Adansonia digitata, Ceiba pentandra,* and *Milicia* (*Chlorophora*) *excelsa* also belong or might have belonged to the upper layer of the original forests.

Further north, with higher elevation and precipitation, more trees appear in the upper story of the dry semideciduous forests: *Celtis philippensis, Celtis zenkeri, Cola gigantea* var. *glabrescens, Lonchocarpus sericeus, Anogeissus leiocarpa, Afraegle paniculata, Afzelia africana,* and other species form the upper canopy which gradually becomes closer. The famous Forêt de la Lama in Benin serves as an example of this type, which corresponds to the Inner Zone subtype of the dry semideciduous forests. It appears noteworthy that the regressive (after removing of the trees) and the initial stages of this forest type are thickets and not grassland, thus reducing the incidence of fires considerably.

Fire is, however, a decisive factor in the third subtype of the dry semideciduous forests, called Fire Zone subtype by Hall & Swaine (1981). This forest type is more or less confined to the northern part of the area, situated between latitudes 7° and 8°N. Here there is only one rainy season. The northern savannas are not far away. The evergreen shrubs of the understory are absent. Instead, many herbaceous species cover the forest floor. The destruction of the forest here often leads to tall grassland interspersed with savanna shrubs and trees including *Piliostigma thonningii, Nauclea latifolia, Daniellia oliveri, Prosopis africana, Pterocarpus erinaceus,* etc. This is the country of the derived or Guinean savannas, which gradually merge into the drier Sudanian savannas north of the 8th parallel.

Fine examples of these forests of the Fire Zone subtype of dry semideciduous forests are to be found near Atakpamé and Blitta in Togo. Trees like *Erythrophleum suaveolens, Afzelia africana, Ceiba pentandra, Diospyros mespiliformis, Pterocarpus erinaceus, Albizia zygia,* and *Aubrevillea kerstingii* compose this type of forest which attains in Togo at least 8.5° northern latitude. Thus, White's (1983) mapping unit 27 of Ghana, Togo, and Benin seems to extend too far to the south. Instead, the situation in these northern parts of the Dahomey Gap resembles more that of the V-Baoulé, a similar interval of the Guinean highforest belt situated in Ivory Coast, and even more that of northern Nigeria, where White uses his mapping unit 12 for the area around Ilorin.

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VEGETATIVE AND REPRODUCTIVE FEATURES OF FOREST AND NONFOREST GENERA OF AFRICAN COMMELINACEAE

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ABSTRACT

A syndrome of vegetative and reproductive characters is present in the forest genera of African Commelinaceae and lacking in the nonforest genera, which exhibit a separate set of attributes. The forest genera characters include the presence of stolons, axillary inflorescences, white flowers, afternoon flowering, and bird-dispersed seeds. The distinctive features of the forest genera seem to be mainly adaptations to low light intensity, while those of the nonforest genera apparently are more related to the availability of water. Both forest and nonforest genera show convergent evolution with regard to the characters examined in this investigation.

RÉSUMÉ

Il existe un syndrome de caractères végétatifs et reproducteurs dans les genres forestiers des Commelinacées africaines mais il fait défaut dans les genres non-forestiers, qui possèdent des traits différents. Parmi les caractères des genres forestiers on remarque la présence de stolons, d'inflorescences axillaires, de fleurs blanches, de floraison après midi et de graines dispersées par des oiseaux. Les traits distincts des genres forestiers semblent être principalement des adaptations à la faible intensité lumineuse tandis que ceux des genres non-forestiers semblent davantage reliés à la présence ou non d'eau. Les genres forestiers et non-forestiers ont une évolution convergente en ce qui concerne les caractères examinés dans cette étude.

While analyzing the phytogeographic relationships of the 17 genera of African Commelinaceae (Faden, 1983a), I found it useful to classify each genus ecologically, based on whether the majority of its species occurred chiefly in forest or nonforest habitats. The ten "forest" genera were found to be mainly West African and Madagascan, while the seven "nonforest" African genera had their greatest development in eastern and central Africa, particularly the areas of the Flora of Tropical East Africa and Flora Zambesiaca.

This dichotomous ecological classification of genera of Commelinaceae has led to the recognition that certain vegetative and reproductive features are frequent among forest Commelinaceae but are rare or lacking in nonforest taxa. Conversely, there are vegetative and reproductive characters that are almost restricted to nonforest taxa. The purpose of this paper is to describe the differences between the forest and nonforest genera and discuss the ecological and taxonomic significance of them.

The focus of this study is the African genera of Commelinaceae. These genera have been selected because they are, for the most part, clearly delimited—unlike many genera in the Neotropics—and they are sufficiently numerous in both forest and nonforest habitats to make generalizations meaningful. In addition, both forest and nonforest genera include members of the tribes Tradescantieae and Commelineae (Faden, 1985), indicating different lineages within both habitat groups (Table 1). Examples from Commelinaceae outside Africa are included when they support the general African patterns or when they show a range of variation not present in Africa.

Following Faden (1983a), the African forest genera of Commelinaceae are *Amischotolype* (syn. *Forrestia*), *Buforrestia, Coleotrype, Palisota, Pollia, Polyspatha, Pseudoparis, Rhopalephora, Stanfieldiella,* and *Tricarpelema* (Table 1). The genera whose species occur mainly in nonforest habitats are *Aneilema, Anthericopsis, Commelina, Cyanotis, Floscopa, Murdannia,* and *Triceratella.* The characters compared between the forest and nonforest genera are habit, vegetative morphology, vegetative reproduction, and sexual reproduction.

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TABLE 1. African genera of Commelinaceae. The genera marked with an asterisk are endemic to Africa and/or Madagascar.

Tribe or Subfamily	Forest Genera	Nonforest Genera
Tradescantieae	*Amischotolype* (syn. *Forrestia*)	*Cyanotis*
	*Coleotrype**	
	*Palisota**	
Commelineae	*Buforrestia*	*Aneilema*
	Pollia	*Anthericopsis**
	*Polyspatha**	*Commelina*
	*Pseudoparis**	*Floscopa*
	Rhopalephora	*Murdannia*
	*Stanfieldiella**	
	Tricarpelema	
Cartonemoideae		*Triceratella**

HABIT, VEGETATIVE MORPHOLOGY, AND VEGETATIVE REPRODUCTION

All species of forest genera of African Commelinaceae are perennials that generally lack dormancy. Underground storage organs are uncommon in these genera, although rhizomes characterize *Palisota* and distal root tubers are present in both species of *Pseudoparis*. Shoots are usually erect to ascending, and stolons are common, occurring in *Buforrestia, Pollia, Polyspatha, Stanfieldiella,* and perhaps other genera. The leaves are spirally arranged, petiolate, generally dark green above, sometimes purple beneath, and not notably succulent. Elsewhere in the tropics, twiners (five genera in Asia and the Neotropics: *Aëtheolirion, Dichorisandra, Porandra, Spatholirion,* and *Streptolirion*) and epiphytes (*Cochliostema* with two species in the Neotropics; *Belosynapsis* with one epiphyte in India) occur in wet forests.

Vegetative reproduction occurs in nearly all forest genera, mainly by means of stolons or rhizomes. Occasionally the species just spread diffusely, the shoots being decumbent, e.g., *Coleotrype laurentii* K. Schum. In a few species, e.g., both species of *Pseudoparis,* vegetative reproduction is apparently lacking.

Habits among the seven nonforest genera are variable. Annuals are frequent, occurring in all of these genera except the monotypic *Anthericopsis*. They are particularly common in *Aneilema,* in which about one-third of the approximately 56 African species are annual (Faden, 1975).

The perennials within the nonforest genera differ from those of the forest genera in a number of features. Nearly all of the former have a dormancy, either obligatory (i.e., plants will not grow continuously) or facultative (i.e., plants will grow as long as suitable climatic conditions prevail). In most nonforest perennials the persistent parts are underground and the aerial flowering shoots are annual: *Anthericopsis sepalosa* (C. B. Clarke) Engl. and species of *Aneilema, Commelina, Cyanotis,* and probably *Murdannia*. Specialized, subterranean storage organs are common in this group and include tuberous roots (*Anthericopsis, Aneilema, Commelina,* and *Cyanotis*), rhizomes (*Aneilema, Commelina,* and *Cyanotis*), bulbs (*Cyanotis*), and corms (*Cyanotis*), although the latter two types are decidedly uncommon. In a few nonforest perennials (e.g., *Aneilema rendlei* C. B. Clarke) the plants die back to a persistent aerial base during the dry season, with no significant storage underground.

The forest species of the nonforest genera are generally decumbent and usually lack dormancy except in forests with a pronounced dry season. They lack underground storage organs.

Shoots in nonforest genera vary from erect to decumbent or repent. Leaves may be spirally arranged (e.g., most species of *Aneilema*) or distichous, as in nearly all species of *Commelina*. Both arrangements occur in some species (e.g., *Aneilema indehiscens* Faden). The leaves may be petiolate, but are often sessile, as in all species of *Murdannia* and *Cyanotis*. Infrequently the leaves are cordate or amplexicaul at the base (e.g., *Commelina latifolia* A. Rich.).

In most nonforest species the leaf is not distinctly succulent, but succulent leaves occur in nearly all species of *Cyanotis* and *Murdannia* and in a few of *Aneilema*. Succulence is manifested in an adaxial hypodermis in *Cyanotis* and *Murdannia* (Tomlinson, 1966, 1969) but in an enlarged adaxial epidermis in *Aneilema* (Tomlinson, 1966; Faden, 1975).

True twiners and epiphytes are absent among the nonforest taxa.

In the nonforest genera vegetative reproduction is often lacking in the annuals and in the perennials with definite bases. When it occurs in the latter, it is usually by means of offsets or forking rhizomes. The majority of species that have vegetative reproduction are perennials lacking definite bases. They spread by means of decumbent to repent stems. These occur in species of *Aneilema, Commelina, Cyanotis,* and *Floscopa*. Stolons are never produced.

Sexual Reproduction

The most striking features of sexual reproduction that characterize forest genera are axillary inflorescences, white flowers, late-opening flowers, and seed dispersal by frugivorous birds. Strictly axillary inflorescences occur in all species of *Amischotolype, Buforrestia, Coleotrype,* and in some species of *Palisota* (Brenan, 1984), *Pseudoparis* (Perrier de la Bâthie, 1936, 1938) and *Stanfieldiella* (Morton, 1967; Brenan, 1968). In genera such as *Buforrestia* and *Coleotrype* the inflorescences always emerge through a hole at the base of the sheath of the subtending leaf. Among non-African forest genera, solely axillary inflorescences also distinguish the neotropical *Campelia, Cochliostema, Geogenanthus,* and an undescribed genus. They are also characteristic of a number of South American species of *Dichorisandra*.

Strictly axillary inflorescences are rare in nonforest genera, defining none of them, but rather occurring in isolated species such as *Aneilema zebrinum* Chiov. [syn. *Ballya zebrina* (Chiov.) Brenan] and an undescribed species of *Cyanotis* (Faden & Suda, 1980).

White-flowered species are common among the forest genera. All or most species of *Buforrestia, Palisota, Pollia, Polyspatha,* and *Stanfieldiella* have white or whitish flowers. In addition, two (of nine) species of *Coleotrype* and at least one (of two) species of *Pseudoparis* are white-flowered. Curiously, the three African forest genera that do not have white-flowered species, *Amischotolype, Rhopalephora* and *Tricarpelema,* are all mainly Asiatic in distribution with single, widely disjunct species in Africa (Faden, 1983a).

White flowers are rare or uncommon among the nonforest genera, being mainly restricted to the forest species of these genera. The predominant flower colors are blue or pink to purple or violet. Yellow-flowered species occur in four genera (*Aneilema, Commelina, Floscopa,* and *Triceratella*) and buff- to orange-flowered species occur in several evolutionary lines within *Commelina*.

Commelinaceae flowers are open only during daylight hours, and flowers of each species have characteristic opening and closing times. In *Aneilema* it has been shown that related, sympatric species may sometimes be isolated by flowering at different times of day (Faden, 1983b). Although much of the published information on flowering times is incomplete and anecdotal, a survey of flowering times of the Commelinaceae of West Africa (Brenan, 1968) indicates that flowers of forest genera species rarely if ever open before 10:00 A.M., and in many species they open only in the afternoon. In contrast, most species of the nonforest genera have flowers open before 10:00 A.M., many opening by 7:00 A.M., and fade by noon. There are some exceptions: a few species of *Aneilema* flower in the afternoon, and species of *Murdannia* usually have relatively late-opening flowers for a nonforest genus.

Adaptations for seed dispersal by frugivorous birds are present in several African forest genera. Brightly colored berries characterize the endemic genus *Palisota*. Crustaceous, lustrous, blue to lead-colored, berrylike fruits are present in all species of *Pollia*. Bright red arils cover the seeds of the Asian species of *Amischotolype,* but it is not clear whether they also occur in the single African species of the genus. All of these adaptations for frugivory also occur in non-African forest genera of Commelinaceae. In addition, there are seemingly mimetic seeds in one species of the Asian *Spatholirion* and a "pseudoberry" formed by the fleshy, accrescent sepals in the neotropical *Campelia zanonia* (L.) HBK (Faden, unpubl.).

With the possible exceptions of single, undescribed species of *Commelina* from Madagascar and Ecuador (Faden & Hunt, 1987) respectively, adaptations for frugivory are lacking in the non-

forest genera. These genera typically have small seeds that lack any obvious means of dispersal.

Discussion

The occurrence of a suite of vegetative and reproductive characters in the forest genera of African Commelinaceae that are individually rare or uncommon and in combination are totally lacking in species of nonforest genera leads to two questions. What is the possible adaptive significance of the features that are common in forest genera? What is the evolutionary significance of this concordance of characters in such a diversity of genera?

The key to an understanding of the adaptive significance of the vegetative and of some of the reproductive characters of the forest taxa is, I believe, the fact that these species grow in the forest understory where light intensity is low. The erect habit with spirally arranged leaves permits the shoots to reach a maximum height with a maximum leaf surface exposed to the light. Similarly, the climbing and epiphytic habits present in some Asian and neotropical forest Commelinaceae are best explained as adaptations for receiving more light. Stolons allow the spacing of the erect shoots through the production of prostrate leafless stems (stolons) as opposed to energetically more expensive leafy shoots. The red or purple lower leaf surface in such species as *Polyspatha paniculata* Benth. probably increases photosynthetic efficiency (Lee et al., 1979). Axillary inflorescences permit sexual reproduction without the production of additional vegetative growth, which would be energetically wasteful. At the same time, axillary inflorescences allow the vegetative shoots to continue normal growth.

Low light intensity probably also explains the predominance of white flowers among the forest species, the white color providing a strong contrast with the dull background and deep shadows of the forest floor. The absence of strong sunlight might account for the frequency of afternoon flowering in the forest taxa, although there are no data showing that the avoidance of the strong midday sun has been a selective factor for morning flowering in the nonforest genera. Despite the more moderate growing conditions in the forest understory, there is also no evidence that forest species have longer daily flowering times than nonforest species. Conversely, the availability of all the daylight hours for flowering in forests could permit more species to coexist by having short, nonoverlapping flowering times, but the only example of this is in the genus *Stanfieldiella* in which *S. imperforata* (C. B. Clarke) Brenan and *S. oligantha* (Mildbr.) Brenan have short, discrete flowering times (Brenan, 1968).

The presence of adaptations for seed dispersal by fruit-eating birds among the forest genera of African Commelinaceae reflects the pattern for the family as a whole in wet tropical forests. Some forest genera of tropical Asian and American Commelinaceae also exhibit such adaptations. Several authors have noted that fleshy diaspores are the dominant dispersal type in wet tropical forests for flowering plants in general (Gentry, 1983; Opler et al., 1977, 1980). The Commelinaceae also show this trend (Faden, unpubl.).

In contrast to understory plants that grow in wet tropical forests, where light seems to be the major limiting factor, plants growing in seasonally dry, tropical, nonforest habitats seem to be mainly limited by the availability of water. Primary adaptations in habit and vegetative morphology such as the annual habit, dormancy accompanied by underground storage organs, and succulent foliage and stems enable the plants to survive the dry season. Less obvious are the adaptations that protect delicate buds, floral parts, and developing fruits from desiccation. These include the spathes of *Commelina,* which are often filled with liquid, and the glandular bracts, bracteoles, and sepals of *Aneilema* species (Faden, 1975).

The forest species of nonforest genera may exhibit some of the characters of the forest genera species but they never show all of them. For example, flowers of *Aneilema umbrosum* (Vahl) Kunth and *Commelina longicapsa* C. B. Clarke are white, but the plants are not stoloniferous. None of these species has strictly lateral inflorescences.

The interpretation of the evolutionary significance of the syndrome of characters in the forest genera depends upon our knowledge of generic relationships. I recently published an outline of a revised classification of the family that recognized two subfamilies, Cartonemoideae and Commelinoideae, with the Commelinoideae divided into two tribes, Tradescantieae and Commelineae (Faden, 1985). The tribes Tradescantieae and Commelineae are defined on characters

of the pollen grains and stomata, and thus their generic composition is very different from tribes of the same names as used by earlier authors [e.g., Clarke (1881), Brückner (1926), Woodson (1942), and Rohweder (1956)], who separated them on number of fertile stamens, floral symmetry, or inflorescense structure. The new taxonomy of the family is much more natural than previous classifications.

Under the system of Faden (1985), the 17 African genera of Commelinaceae include the single cartonemoid genus *Triceratella*. The remaining genera comprise both Tradescantieae and Commelineae (Table 1). Most important to the present investigation is that the African Tradescantieae and Commelineae both contain forest and nonforest genera. Thus, assuming that these tribes are monophyletic, the occurrence of a similar suite of adaptive characters in forest genera of both Tradescantieae and Commelineae would be best explained by convergent evolution.

The African forest genera of Tradescantieae and Commelineae are very similar in their vegetative morphology. The only significant difference is that the stoloniferous habit is not known for certain in any of the Tradescantieae. Among the reproductive characters discussed above, both tribes include genera with exclusively lateral inflorescences, predominantly or solely white flowers, mainly afternoon-flowering species, and fruits dispersed by frugivorous birds.

Conversely, when the character states of the vegetative and reproductive characters discussed above are examined in *Cyanotis*, the sole nonforest African genus of Tradescantieae, they are found to agree much more closely with those of the nonforest Commelineae than with the forest genera of Tradescantieae. For example, at least two African species of *Cyanotis*, *C. lanata* Benth. and *C. axillaris* (L.) Sweet, are annuals. Nearly all of the perennial species have a dormancy, and most species have underground storage organs. The leaves of many species have a distichous arrangement, at least in part, and both the stems and leaves in all species are succulent and the leaves never petiolate. Flowers are mainly pink to violet and open in the morning.

From the above discussion it may be concluded that habit, vegetative characters, and some reproductive features in the African genera of Commelinaceae have been selected on the basis of the habitat in which the plants grow, particularly whether or not they grow in wet, tropical forests. This selection has occurred in genera of both the Tradescantieae and Commelineae. The great similarity in these characters between forest genera of both tribes is due to convergence.

The analysis used in this paper may have application to other plant families and may be employed at various taxonomic ranks. The criteria necessary for its use are a secure taxonomic foundation, the occurrence of taxa of the same rank (e.g., sections, subgenera, genera) in discrete habitats, and a sufficient number of taxa to exhibit a pattern. The family Acanthaceae in Africa comes to mind for similar analysis because of the large number of genera, many of which are very clearly either forest or nonforest genera, as defined above. A worker more familiar with the taxonomy of that family will have to determine whether it is truly suitable for such an analysis. Friis (pers. comm.) states that the African genera of Urticaceae could usefully be examined in the manner used in this paper.

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DISTRIBUTION PATTERNS AND BIOLOGICAL OBSERVATIONS IN THE URTICACEAE OF SUB-SAHARAN AFRICA, MADAGASCAR, AND THE MASCARENES[1]

IB FRIIS[2]

ABSTRACT

The Urticaceae includes 19 genera and about 140 species in sub-Saharan Africa, Madagascar, and the Mascarenes out of a total of about 50 genera and 1,500 species worldwide. A summary of recent revisional work on African Urticaceae by the author and others is outlined here. The majority of the species dealt with are associated with either lowland forest or various types of upland or montane forest. A few species in this category are narrow local endemics but the majority are widespread. Some have weedy tendencies. Specialized genera are distributed in the drier vegetation types of the Zambezian and Somalia–Masai regions, or even in the desertlike vegetation types of the Karoo–Namib and Sahara regions. Distribution maps of selected species are included to illustrate characteristic distribution patterns. Some general observations on pollination and dispersal biology are outlined and compared with information on habitat.

RÉSUMÉ

Les Urticacées de l'Afrique sub-Saharienne, Madagascar et les Mascareignes comprend 19 genres et environ 140 espèces, sur un total d'à peu près 50 genres et environ 1,500 espèces dans le monde entier. L'auteur fait un résumé du travail de révision récent (par l'auteur lui même et d'autres chercheurs) sur les Urticacées africaines. La majorité des Urticacées africaines sont associées à la forêt, soit de basse altitude ou des types variés de haute altitude ou de montagne. Quelques espèces dans cette catégorie sont des endémiques étroites et locales, alors que la majorité est répandue et que quelques unes ont une tendance à être des mauvaise herbes. Des genres spécialisés sont distribués dans les types de végétation arides du Soudan ou les régions de Zambesi ou du Somali–Massai, ou même dans les types de végétation desertiques des régions de Karoo–Namib ou du Sahara. Des cartes de répartition d'espèces selectionées ont été préparées pour illustrer les types de distribution les plus caractéristiques. L'article comprend des observations générales sur la pollinisation et la biologie de dissémination qui sont comparées avec des informations sur l'habitat.

The Urticaceae comprise some 19 genera and ca. 140 species in sub-Saharan Africa, Madagascar, and the Mascarenes, out of a total of ca. 50 genera and 1,500 species worldwide. The majority of the genera occur in humid tropical lowlands or on humid tropical mountains, but a certain number extend (e.g., *Urtica*) into temperate regions or have their main distribution there. In Africa and western Asia a few genera have adapted to warm and dry habitats, notably *Obetia* and *Forsskaolea*.

The African taxa have been covered in the classical floras of tropical (Rendle, 1917) and southern Africa (Brown, 1925), and later in the modern floras of western and central Africa and Madagascar. The taxa of eastern and southern Africa, largely unstudied since the early part of this century, are now in the process of being revised (Table 1). Recent monographic or revisional work on various parts of the family also include a number of studies of African taxa (Table 2).

On the basis of the cited flora accounts, revisions, and monographs, it is possible to give a reasonably current survey of the family in sub-Saharan Africa, including Madagascar and the Mascarenes. A summary of taxonomic and phytogeographic data (Table 3) includes information about number of species per genus, African and extra-African distribution, notes on habitat or ecology, and a phytogeographical analysis. The nomenclature of the phytochoria used in this analysis is that of White (1983), appropriately abbreviated.

[1] I thank two colleagues at the Royal Botanic Gardens, Kew: Mr. Wessel Marais, for reading the text and commenting on the Mascarene Urticaceae, and Miss C. M. Wilmot-Dear, for checking distribution data. I also thank Dr. Christian Puff, University of Vienna, for commenting on the text.

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TABLE 1. Floristic treatments of Urticaceae in sub-Saharan Africa, Madagascar, and the Mascarenes.

I. The classical floras.	
	Flora of Tropical Africa (Rendle, 1917).
	Flora Capensis (Brown, 1925).
II. Modern floras.	
a.	Published accounts.
	Flore du Congo Belge (Hauman, 1948).
	Flora of West Tropical Africa, 2nd edition (Keay, 1958).
	Flore du Madagascar (Leandri, 1950, 1964).
	Prodromus einer Flora von Südwestafrika (Roessler, 1967).
	Flore du Cameroun (Letouzey, 1968).
	Flore des Mascareignes (Marais, 1982; Marais & Jellis, 1985).
b.	Accounts in press or in preparation.
	Flora of Ethiopia (Friis, ms. completed).
	Flora Zambesiaca (Friis, ms. completed).
	Flora of Tropical East Africa (Friis, ms. completed).
	Conspectus Florae Angolensis.
	Flora of Southern Africa (Friis & Immelman, ms. completed).

PHYTOGEOGRAPHIC OBSERVATIONS

Genera with the majority of species in tropical lowland forest are: *Urera, Laportea, Boehmeria,* and *Phenax*. The distribution of *U. trinervis* (syn. *U. cameroonensis*), an essentially Guineo-Congolian species, is shown in Figure 1 and that of *U. sansibarica,* a Zanzibar–Inhambane species, in Figure 2. Centered in humid upland forests of the tropical parts of the study area are *Girardinia, Pilea, Lecanthus, Elatostema,* and *Procris.* The distribution of the two essentially Afromontane species *G. bullosa* and *G. diversifolia* are shown in Figures 3 and 4. However, the phytogeographical distinction between upland and lowland distributions is not absolute at the generic level, e.g., the existence of the essentially Afromontane *U. hypselodendron* (Fig. 5) in a genus otherwise found in lowland forests.

Some chiefly Afromontane genera have a distribution in lowland areas outside the tropical parts of Africa, Madagascar, and Mascarenes. Thus *Urtica* has two species in northeastern and eastern Africa, two in southern Africa, and its main distribution in the northern temperate zone; *Parietaria* has one widespread high altitude species in the mountains of tropical Africa and Madagascar and its main distribution in the warm temperate regions of the northern hemisphere; *Droguetia* has two species in the African mountains, the rest in southern Africa, Madagascar, and the Mascarenes; and *Australina* has one montane species in Ethiopia, the other in lowlands of Australia and New Zealand. The distribution of the widespread, but essentially Afromontane *Didymodoxa caffra* is shown in Figure 6; the genus as a whole occurs also in southern Africa. *Australina* and *Didymodoxa* are examples of southern genera.

TABLE 2. Recent monographs, revisions, and other taxonomic or nomenclatural publications relating to African Urticaceae.

Australina (Friis and C. M. Wilmot-Dear, in press, a worldwide revision).
Boehmeria (Friis and Marais, 1982, a nomenclatural note).
Didymodoxa (Friis & Wilmot-Dear, in press, a worldwide revision).
Droguetia (Friis and C. M. Wilmot-Dear, in press, a worldwide revision).
Forsskaolea (Merxmueller and Roessler, 1980, taxonomic study of southwestern African taxa; Friis, 1982b, nomenclatural note; Lobin and Roessler, 1985, revision of species on the Canary and Cape Verde Islands, Friis & Wilmot-Dear, in press, additional notes).
Girardinia (Friis, 1981, worldwide revision).
Laportea (Chew, 1969, monograph; Friis, 1981, 1982a, additional taxonomic notes).
Obetia (Friis, 1983, worldwide revision).
Pilea (Friis, in prep., revision of African species).
Parictaria (Friis, 1986b, revision of the nomenclature of the African species).
Pouzolzia (Friis and Jellis, 1984, revision of the African species, Friis, 1986c, two additional taxa).
Urera (Friis, 1982a, taxonomic notes on generic delimitation; Friis, 1985, a revision of the East African taxa).

TABLE 3. Survey of genera of Urticaceae in sub-Saharan Africa, including Madagascar and the Mascarenes.

Genus	Approximate Number of Species in Study Area	Distribution in Sub-Saharan Africa and Madagascar	General Distribution	Habitats	Phytogeographical Element
Urtica	6	Mountains of Ethiopia and East Africa; South Africa	Widespread in temperate and warm temperate regions	Forest edges and grasslands; weedy	Afromontane; ?Kalahari–Highveld
Urera	ca. 15	Widespread in the humid areas of western and central tropical Africa; also along the eastern coast; Madagascar, Mascarenes	Tropical America, tropical Africa, Oceania	Lowland and montane evergreen forest	Guineo–Congolian, Afromontane, Zanzibar–Inhambane, Madagascar, Mascarenes
Obetia	7	Dry areas of northeastern, eastern, south central and southwestern Africa; Madagascar, Mascarenes	Not known elsewhere	Dry bushland or woodland, often on rocky outcrops	Somalia–Masai, Lake Victoria, Zambesian, Kalahari–Highveld, Tongaland–Pondoland, Karoo–Namib, Madagascar, Mascarenes
Girardinia	2	Uplands and montane areas of West, central and East Africa; Madagascar	One species restricted to Africa only; the other also throughout warm Asia	Upland and montane forest, especially clearings and margins; weedy	Afromontane, Madagascar
Laportea	16	Widespread throughout the more humid parts of tropical and southern Africa; Madagascar	Genus widespread throughout the tropics	Lowland and upland forest, especially in clearings and at margins; often weedy; a concentration of local endemics on Madagascar	Guineo–Congolian, Afromontane, Zanzibar–Inhambane, Tongaland–Pondoland, Cape, Madagascar
Pilea (incl. *Neopilea*)	ca. 50	Widespread in the humid parts of tropical Africa; Madagascar; Mascarenes	More than 200 species throughout the tropics	Mainly in upland evergreen forest, often at streams; many local endemics, about half of which on Madagascar and the Mascarenes (18 endemic species on the latter islands alone)	Chiefly Afromontane, Madagascar, Mascarenes

TABLE 3. Continued.

Genus	Approximate Number of Species in Study Area	Distribution in Sub-Saharan Africa and Madagascar	General Distribution	Habitats	Phytogeographical Element
Lecanthus	1	At higher altitudes in Cameroon and Ethiopia	Monotypic genus, only species distributed from Africa to Oceania	Moist places in montane evergreen forest	Afromontane
Elatostema	ca. 8	Widespread in the humid parts of tropical Africa; Madagascar; Mascarenes	About 500 species in tropical Asia and in Oceania	Moist places in montane evergreen forest (0–900 m in Mascarenes); species mostly widespread	Afromontane, Madagascar, Mascarenes
Procris	2	At higher altitudes in Cameroon and East Africa, from Kenya to Mozambique; Madagascar; Mascarenes	About 10 species in tropical Asia, the African species extend to Indonesia and the Philippines	Moist places in upland and montane evergreen forest (0–800 m in Mascarenes)	Afromontane, Madagascar, Mascarenes
Boehmeria	2	Humid lowlands of West, Central and East Africa, from Ethiopia to Zimbabwe; Madagascar; Mascarenes	About 50 species, distributed in all parts of the tropics; the African species extend to Indonesia; one species endemic on Reunion	Lowland evergreen forest, often at margins and streams (600–1,400 m on Reunion)	Guineo–Congolian, Madagascar, Mascarenes
Pouzolzia	ca. 14	Widespread in tropical and southern Africa; Madagascar	About 60 species, distributed in all parts of the tropics	Ecology very varied, see text; most species widespread, a few narrow endemics	Guineo–Congolian, Afromontane, ?Somalia–Masai, Zanzibar–Inhambane; Zambesian, Kalahari–Highveld, Karoo–Namib, Madagascar, Mascarenes
Pipturus	1	Mountains of the Comoro Islands	About 25 species in Indonesia, Australia, and Oceania; the African species is distributed throughout the range of the genus	Humid upland forest	Madagascar

TABLE 3. Continued.

Genus	Approximate Number of Species in Study Area	Distribution in Sub-Saharan Africa and Madagascar	General Distribution	Habitats	Phytogeographical Element
Debregeasia	1	Montane areas of Ethiopia	About 5 species distributed in the mountains of tropical Asia; the African species extends to the Himalayas	Montane evergreen bushland and forest	Afromontane
Phenax	3	Humid lowland areas of Madagascar and Mascarenes	About 20 species in tropical America; one species in Burma	Humid lowland forest; the species appear to be narrow endemics but are poorly known	Madagascar
Parietaria	1	Montane areas of Cameroon, eastern Zaire, and East Africa, from Ethiopia to Tanzania; Madagascar	About 10 species, widespread in the tropical mountains and the warm temperate regions; the African species extends to Oceania	High altitude evergreen forest, bushland and grassland; very polymorphic	Afromontane
Forsskaolea	5	Dry areas of northern, northeastern, southern, and southwestern Africa; Madagascar; Macaronesia	5 species, of which the northern African species extends to Europe and western Asia	Subdesert vegetation; dry bushland; some species widespread; those of Macaronesia rather narrow endemics	Sahara, Somalia–Masai, Kalahari–Highveld, Karoo–Namib, Cape, Madagascar, Macaronesia
Droguetia	7	Southern Africa and uplands of eastern Africa; north to Ethiopia; Madagascar; Mascarenes	7 species, one African species extends to Indonesia	Upland forest, evergreen bushland; the Mascarene and southern African species rather narrow endemics	Afromontane, Tongaland–Pondoland, Cape, Madagascar, Mascarenes
Australina	1	Ethiopia, Kenya	Two species, one in Ethiopia, the other in southern Australia and New Zealand	Upland evergreen forest, evergreen bushland	Afromontane
Didymodoxa	2	Southern Africa and uplands of East Africa, north to Ethiopia	Endemic on the African mainland	Bushland, edges of evergreen forest	Afromontane, Tongaland–Pondoland, Karoo–Namib, Cape

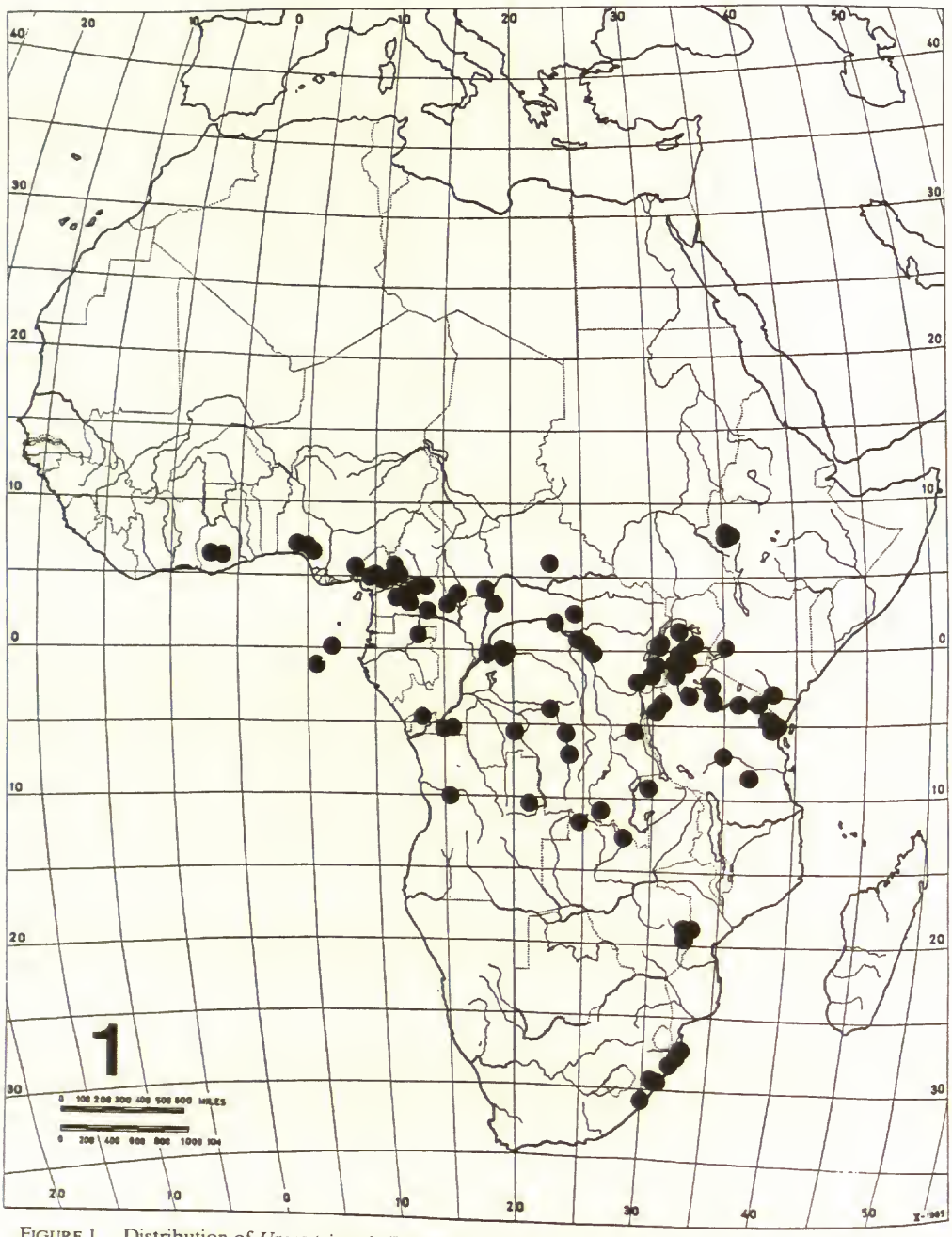

FIGURE 1. Distribution of *Urera trinervis* (Hochst.) Friis & Immelman (syn. *U. cameroonensis* Wedd.).

The most interesting genera phytogeographically are those distributed in the arid zones of Africa and Madagascar. Dry country genera are rare in Urticaceae and include *Pouzolzia, Obetia,* and *Forsskaolea*. The least specialized example is found in *Pouzolzia* (Friis & Jellis, 1984), in which there is a wide range of distribution types, from typical Guineo–Congolian distributions (e.g., *Pouzolzia denudata,* which occurs from the Ivory Coast to the Central African Republic, and south to Angola and Zaire), or Zanzibar–Inhambane distributions (e.g., the narrow endemic *P. fadenii,* only known from the coastal zone of Kenya). There are slightly transgressing patterns

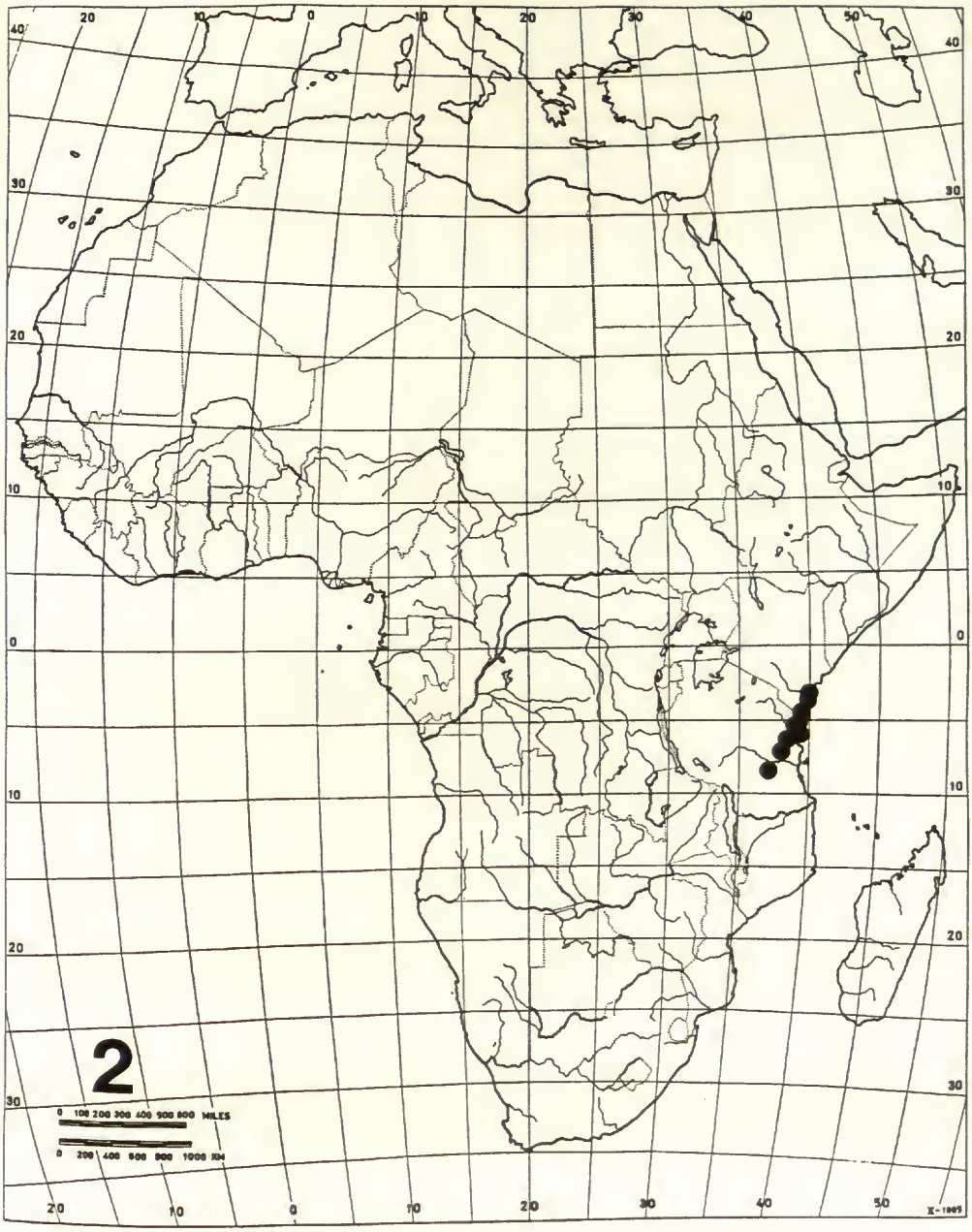

FIGURE 2. Distribution of *Urera sansibarica* Engl.

(e.g., *P. guineensis,* which is basically Guineo–Congolian and distributed from Senegal to Ethiopia, and south to Angola and Tanzania, but also occurs in the surrounding woodland regions). There are Afromontane distributions (e.g., *P. parasitica,* which occurs on Mt. Cameroon, in Ethiopia, and the mountains of eastern and central Africa to Natal, but also occurs in woodland regions in Tanzania and Zambia). And finally there is the arid zone distribution type exemplified by *P. mixta* (syn. *P. hypoleuca*) (Fig. 7). In the northeastern part of its range, *P. mixta* appears to be restricted to the lower part of the Afromontane region, verging on the Somalia–

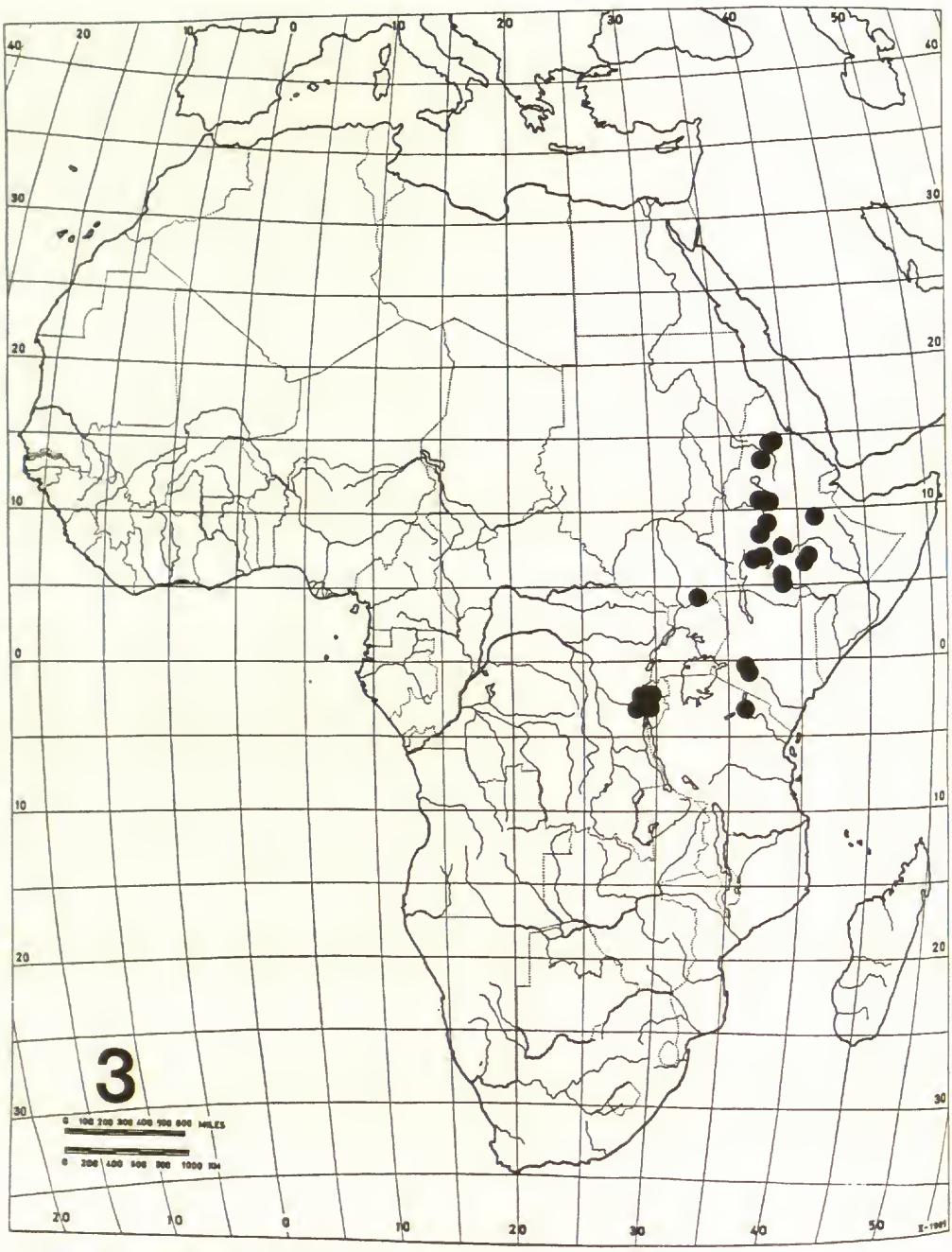

FIGURE 3. Distribution of *Girardinia bullosa* (Steud.) Wedd.

Masai region, where it occurs in rocky places and gorges. In Kenya the species is apparently absent, but it reappears in the drier part of Tanzania and is rather common on dry rocky outcrops in the Flora Zambesiaca area, chiefly in the Zambezian region, but with extensions into the Kalahari-Highveld region. Similar dry country adaptations are found among the species of *Pouzolzia* on Madagascar, but their taxonomy is not yet clear.

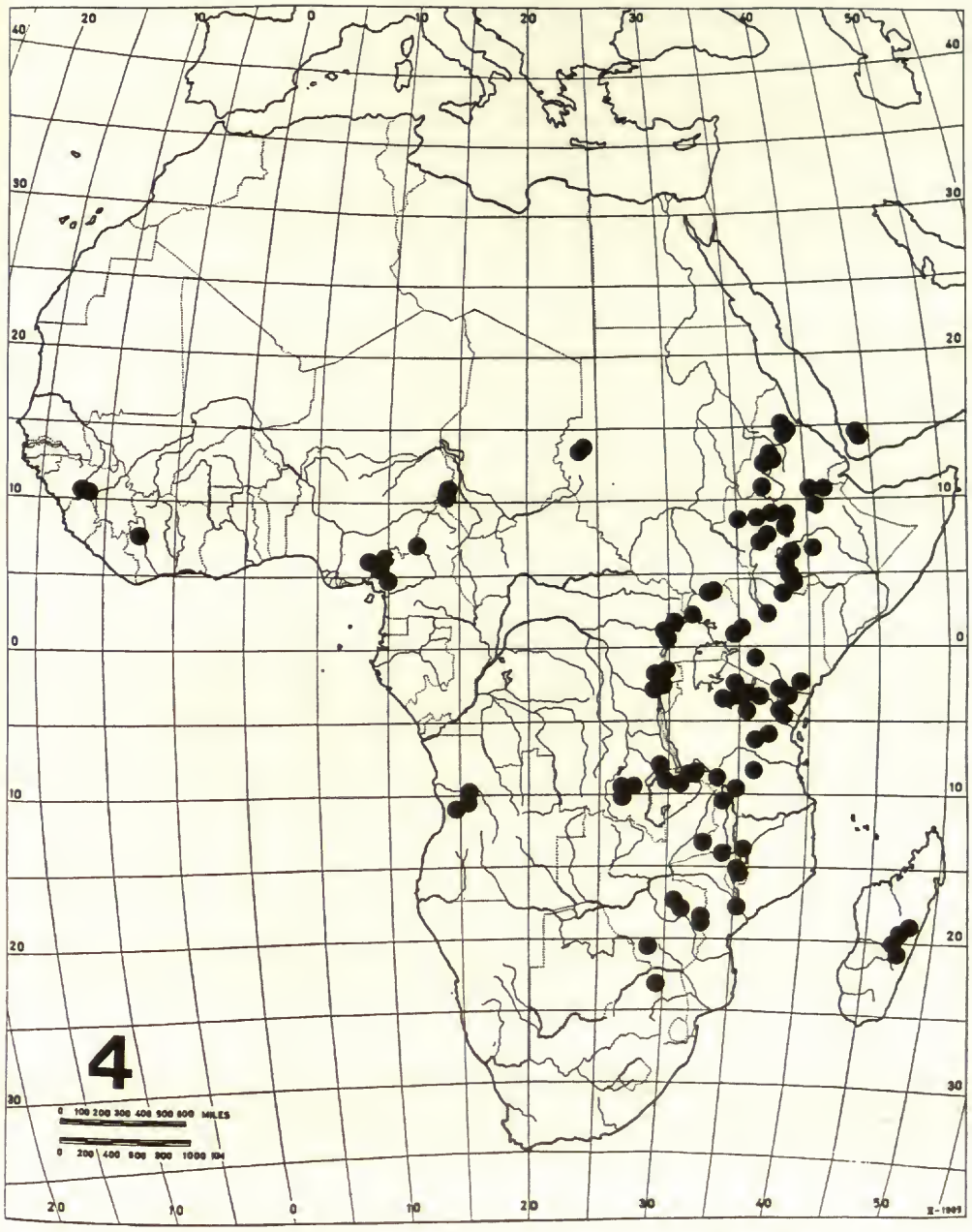

FIGURE 4. Distribution in Africa and on Madagascar of *Girardinia diversifolia* (Link) Friis.

Entirely restricted to the arid zones, at least on mainland Africa, are the species of *Obetia* (Fig. 8). *Obetia* sp. A. is imperfectly known, as only male flowers are extant in herbarium material, but the species could be a narrow endemic of the Somalia–Masai region. *Obetia radula* occurs at rocky outcrops in East Africa, the Somalia–Masai, and Lake Victoria regions, as well as in the drier central and northern part of Madagascar. *Obetia tenax* is distributed in the Zambezian,

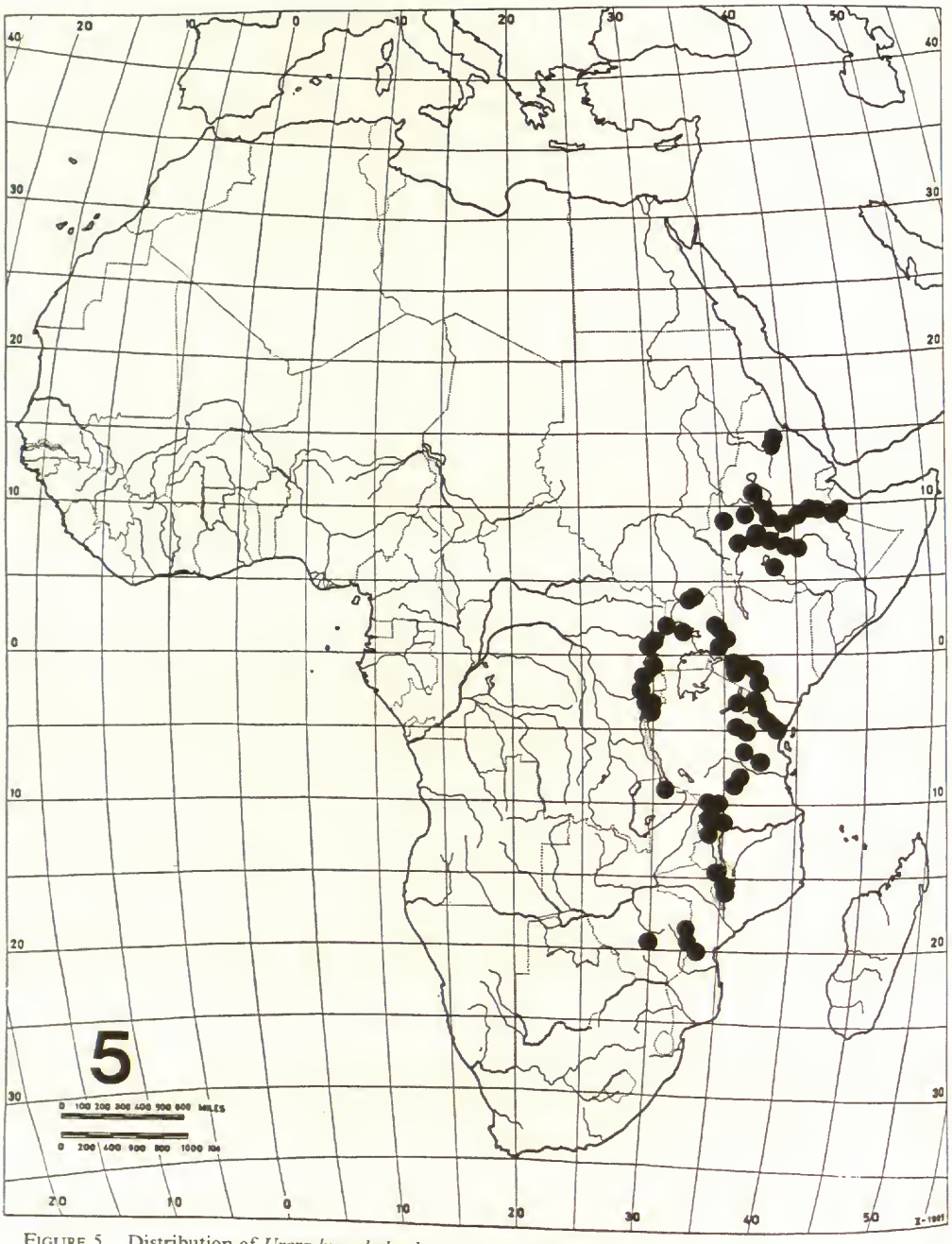

FIGURE 5. Distribution of *Urera hypselodendron* (A. Rich.) Wedd.

Kalahari–Highveld, and Tongaland–Pondoland regions. *Obetia carruthersiana* is essentially distributed in the Karoo–Namib region. The remaining species occur on Madagascar, Aldabra, and the Mascarenes, some in more humid habitats.

Forsskaolea is restricted to arid zones. *Forsskaolea tenacissima* is chiefly Saharan, with extensions to southwest Asia, Europe, and Ethiopia. *Forsskaolea viridis* is disjunct between the Somalia–Masai and the Karoo–Namib regions, and has recently been recorded from the Cape

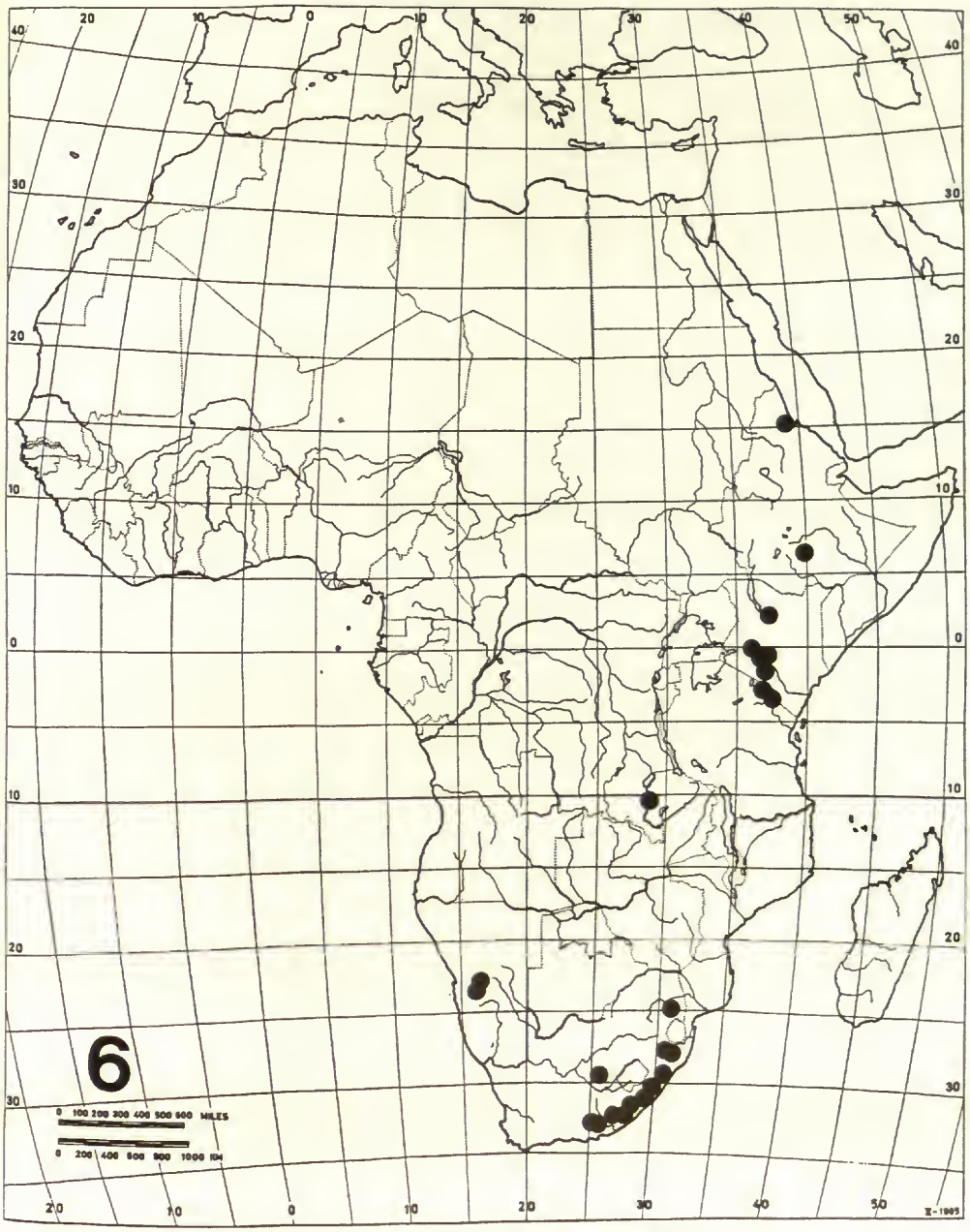

FIGURE 6. Distribution of *Didymodoxa caffra* (Thunb.) Friis & Wilmot-Dear.

Verde Islands (Lobin & Roessler, 1985). With a taxonomic delimitation as proposed by Merxmueller & Roessler (1980), it is restricted to the inland parts of the Karoo–Namib, while *F. hereroensis* occurs on the coast. *Forsskaolea candida* is also basically an inland species, which occurs chiefly in the Cape region and extends into the Karoo–Namib region, where it partly overlaps and intergrades with the two previously mentioned species. *Forsskaolea procridifolia* is restricted to the Cape Verde Islands and *F. angustifolia* to the Canary Islands.

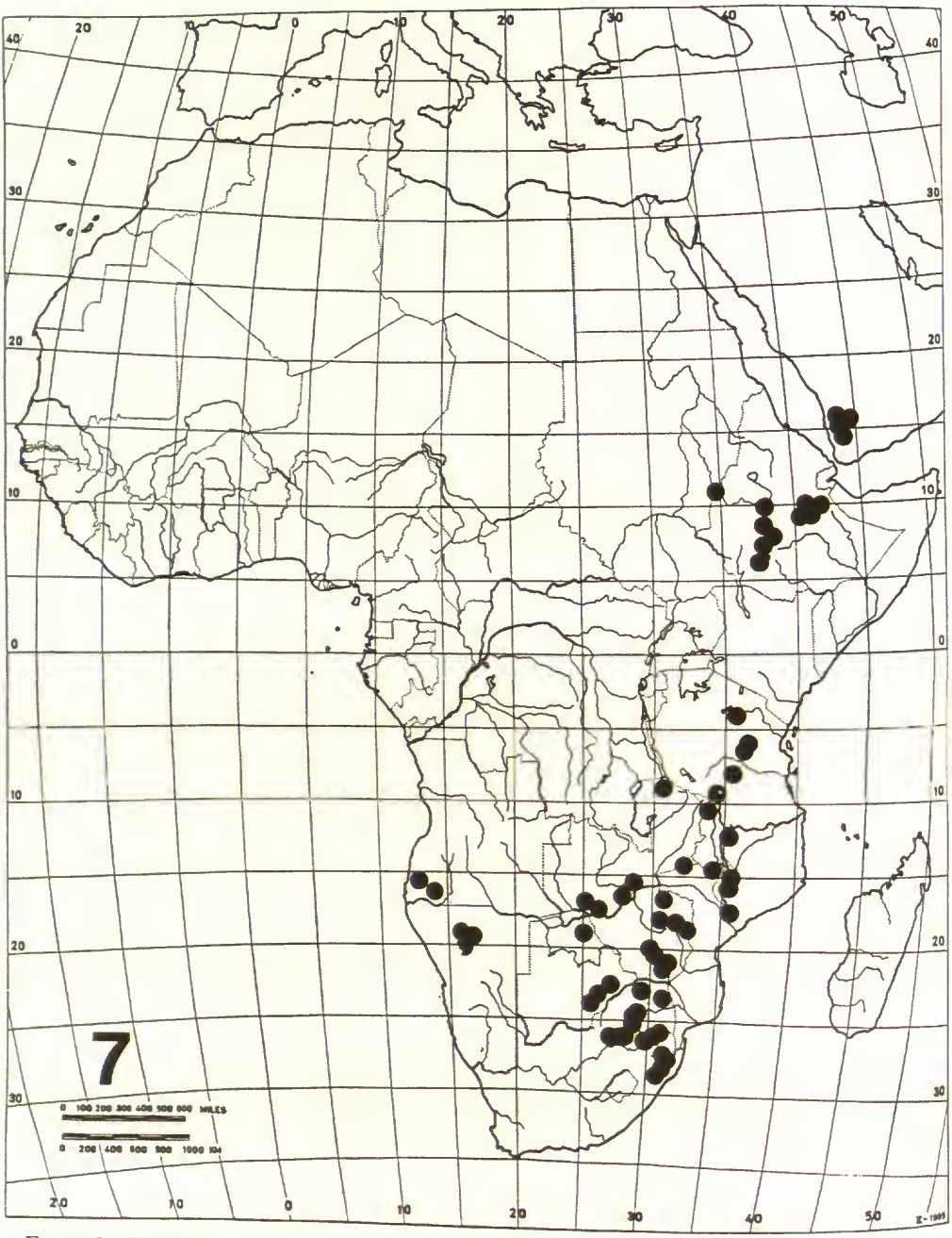

FIGURE 7. Distribution of *Pouzolzia mixta* Solms-Laub.

The genus *Pilea* seems to have more local endemics in the humid Afromontane region, Madagascar, and the Mascarenes than other genera of Urticaceae. However, there is a certain degree of local endemism in the Zanzibar–Inhambane and the Tongaland–Pondoland regions, as shown by *Pouzolzia fadenii* and several taxa of *Laportea*. The latter genus has also radiated considerably in Madagascar.

OBSERVATIONS ON POLLINATION BIOLOGY

Urticaceae are usually said to be entirely or predominantly wind-pollinated (Engler, 1889;

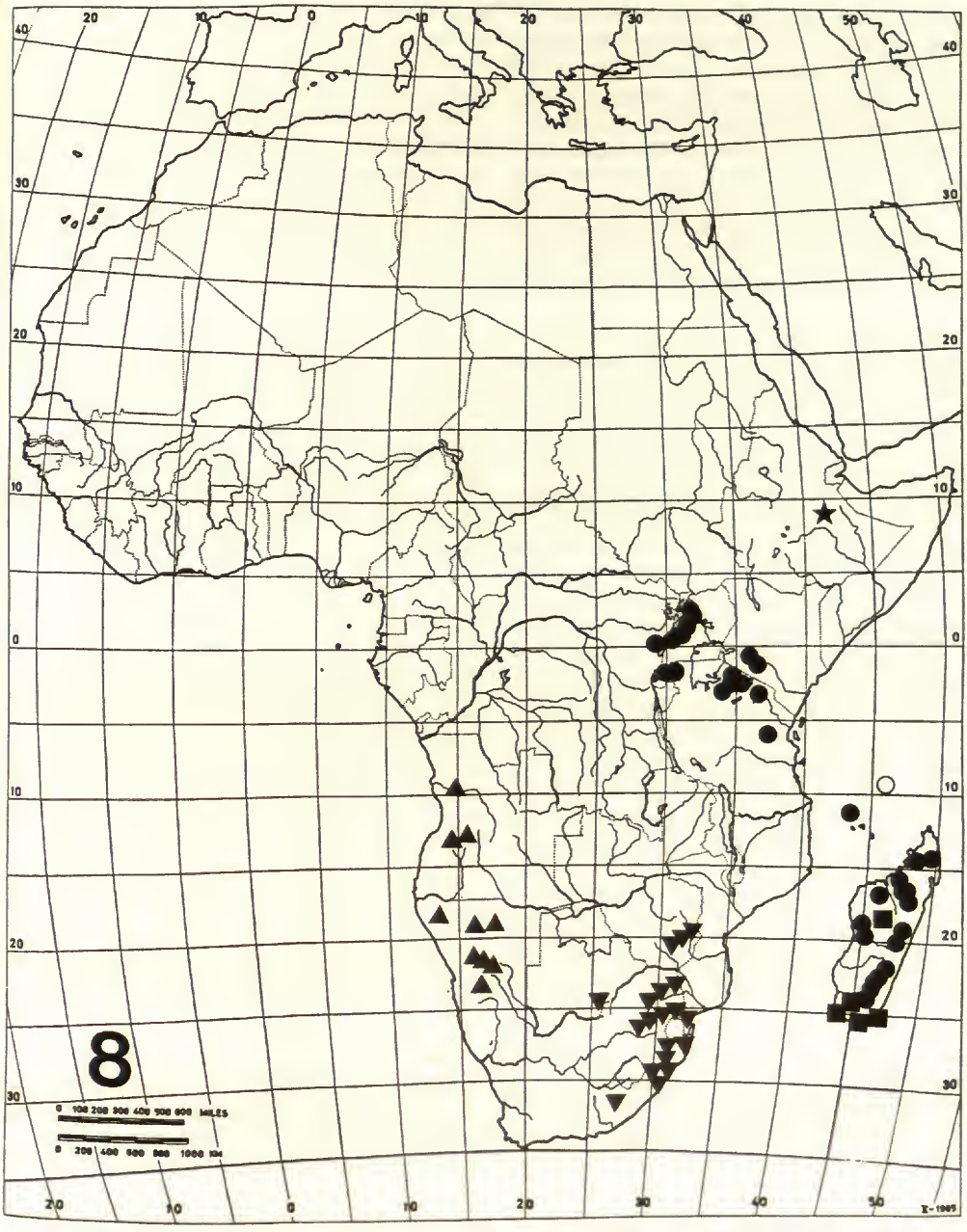

FIGURE 8. Distribution of species of *Obetia* Gaud. Dots: *O. radula* (Bak.) Jackson. Squares: *O. madagascariensis* (Lam.) Wedd. Circle: *O. aldabrensis* Friis. Triangles pointing upwards: *O. carruthersiana* (Hiern) Rendle. Triangles pointing downwards: *O. tenax* (N. E. Br.) Friis. Star: *O.* sp. A. The distribution of *O. ficifolia* (Savigny) Gaud., only on the Mascarene Islands, is not shown.

Leandri, 1964; Faegri & van der Pijl, 1979). All African species have active ejection of the pollen by sudden reflexion of the initially inflexed stamens in the male flowers. The stigmas are typically those of wind-pollinated plants, often penicillate or long and filiform, with a unilateral stigmatic part. The flowers are unisexual with the exception of the occasionally bisexual flowers in *Parietaria*. Plants are usually monoecious (male and female flowers frequently occur in the same inflorescence), although there are some dioecious species.

In the calm air of the humid forest, the active ejection of pollen is obviously of considerable importance for successful pollination, whether it results in pollination of a flower on the same or a neighboring individual. It is therefore interesting to record that genera typical of the lower story of the forest or of the forest floor, such as *Elatostema, Procris, Pilea, Lecanthus, Boehmeria,* and *Droguetia,* and to a certain degree *Girardinia,* and a number of species of *Laportea* and *Pouzolzia* are monoecious, and have active dispersal of pollen from a few male flowers over the female part of the inflorescence or over other inflorescences. These species of Urticaceae can therefore in a certain sense be described as having biotic rather than strictly wind pollination. In the terminology of Faegri & van der Pijl (1979), autogamy is the system where pollen from one flower is actively transferred to the stigma of the same flower. Geitonogamy is the term for a system where pollen is transferred (by a biotic or a nonbiotic agent) between neighboring flowers of one and the same plant, while transfer between flowers on neighboring plants is called xenogamy. There is no special term for the particular type described above, where male flowers pollinate female flowers in other parts of the same inflorescence or on the same (or neighboring) plant.

A better terminology, which would also cover the situation in many Urticaceae, is this: allogamy is taken to include all cases of transfer of pollen from one flower to the stigma of a flower of another plant (xenogamy is considered a special case of this). Autogamy is taken to include all cases of transfer of pollen from one flower to a stigma in a flower on the same plant. In this terminology geitonogamy becomes a special case of autogamy, while autogamy in the strict sense includes transfer of pollen within one flower. Provided there is no self-incompatibility system (which seems unlikely), geitonogamy ensures the successful reproduction of these forest floor genera in the Urticaceae.

As opposed to the species of the closed forest, those which flower in the open, such as *Urera, Obetia,* and most species of *Urtica,* are dioecious. Most species of *Urera* are true lianas that flower only when they reach the canopy, and their pollen is therefore more easily transported by the wind over longer distances. The African species of *Urera* can therefore be regarded as truly wind pollinated. Species of *Obetia* are shrubs or small trees which usually flower long before the leaves develop, and as they grow in very exposed situations there is no difficulty in wind transport of pollen in this genus either. The pollination biology of African species of *Urtica* is poorly known, but in temperate areas pollen of *Urtica* is very frequent in the air far away from flowering populations of *Urtica* (Proctor & Yeo, 1973). Temperate species of *Urtica* must therefore be regarded as truly wind pollinated, and the same probably applies to the African species.

Dispersal of Diaspores

In a number of species of African Urticaceae the persistent perianth becomes fleshy as the fruit ripens. In *Urera,* as a forest climber which reaches the canopy, the diaspore is a berrylike structure, consisting of the achene enclosed in the fleshy, red, or orange persisting perianth. This must be an adaptation to endozoic dispersal, probably ornithochory (as defined by van der Pijl, 1982). A similar situation is found in *Hoslunda* (Lamiaceae), where the fruits are enclosed by the fleshy, orange-red calyx.

Similarly, the genus *Debregeasia* develops fleshy, colored perianths, but here the individual flowers in a cluster fuse laterally, and a fleshy composite fruit is formed. Again endozoic ornithochory must be assumed and is supported by the occurrence of *Debregeasia* in forest clearings or along forest edges where the diaspores can easily be observed by birds. Similar mechanisms may exist in some species of *Laportea,* where the persistent female perianth has been recorded by collectors to become somewhat fleshy in the lower part. These observations require confirmation.

Another kind of animal-aided dispersal, epizoochory, possibly takes place in *Pouzolzia, Boehmeria,* and *Parietaria,* where the persistent perianth or bracts are covered with stiff, sometimes hooked hairs, apparently well suited to adhere to animal fur or to clothing. The diaspore

TABLE 4. Summary of dispersal/diaspore data for genera mentioned in text.

Dispersal	Diaspore	Genus
A) Endozoochory (ornithochory)	a) Red or orange, ± fleshy perianth with enclosed achene.	*Urera*
	b) Infrutescence of several fused, ± fleshy perianths with enclosed achenes.	*Debregeasia*
B) Epizoochory	a) Fruit enclosed in dry, persisting perianth with hooks.	*Pouzolzia, Boehmeria, Parietaria*
	b) Groups of fruits enclosed by bracts with hooks.	*Pouzolzia*
C) Autochory (active ballists, see text)	Achenes	*Pilea, Elatostema, Lecanthus*
D) Anemochory	Winglike perianth with achene.	
1) Winged flyers	Whole inflorescence with several achenes enclosed by winglike bracts.	*Obetia*
2) Winged rollers		*Forsskaolea*
3) Anemoballists (see text)	Achene	*Girardinia*

may here be the individual achene or all or part of whole inflorescences.

Active dispersal occurs in forest floor genera such as *Pilea, Lecanthus,* and *Elatostema.* In these genera an active ejection of the achenes takes place by sudden reflection of inflexed staminodes of the female flowers. This process would, in the terminology of van der Pijl (1982), be classified as actively ballistic autochory. It is homologous with the active ejection of the pollen in the male flowers. A similar active ejection mechanism of the diaspore occurs in the African forest floor genus *Dorstenia* (Moraceae). Here, however, the active ejection of the hard endocarp containing the seed takes place by shrinkage of the fleshy exocarp.

A different type of dispersal is found in *Girardinia,* where the withered female inflorescences form dense spongy structures composed of peduncles, pedicels, bracts, and perianths, which tend to retain many achenes until violently shaken, e.g., by wind. This seems to be a sort of "censer"- or "caster"-like structure, functioning in a way that resembles the wind-shaking mechanisms known from annual or biennial plants in temperate climates (e.g., species of *Papaver*), a syndrome called anemoballistic (van der Pijl, 1982).

Wind dispersal occurs in the desert and woodland genera such as *Forsskaolea* and *Obetia.* In these genera wings have developed to facilitate dispersal by the wind, anemochory. In *Obetia* the wings consist of the accrescent membranaceous tepals, and the diaspore consists of the achene and the winglike enlarged perianth. The diaspores of *Obetia* are small and probably fly rather easily in the wind. In *Forsskaolea* the wings are made up of the large bracts enclosing the inflorescences or partial inflorescences, and the diaspore consists of the whole or part of the inflorescence, with one–several achenes and the winglike bracts. *Forsskaolea* diaspores are comparatively heavy and are probably rolled by the wind. In certain species of *Laportea* the pedicels develop wings; the diaspore consists of fruit and pedicel. Wind dispersal must also be assumed in these species.

These few biological remarks (summarized in Table 4) cover only a selection of African Urticaceae and are based entirely on casual observations in the field or on my observations during herbarium studies. The small size of the flowers of Urticaceae makes it absolutely necessary that careful observations be made and that the structure of flowers and inflorescences are understood. The forthcoming flora works and revisions should facilitate the understanding of the structures involved. With these tools, I am sure that closer biological studies of African Urticaceae by field observers would be rewarding.

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FOREST TREES OF NORTHEAST TROPICAL AFRICA (ETHIOPIA, DJIBOUTI, SOMALIA)—AN ATLAS PROJECT[1]

IB FRIIS[2]

ABSTRACT

For some years the author has worked on taxonomic revisions of species of forest trees occurring in Ethiopia, Djibouti, and Somalia, and on the compilation of distribution data, habitat range, etc. The work has been concentrated on species known to reach a height of 8 m or more. Presumed endemics have been given particular attention. About 200 species have been found to fulfill the criteria for inclusion. Distribution maps of the species have been prepared. Phytogeographical analyses of the various elements in the forest tree flora are under preparation.

RÉSUMÉ

L'auteur travaille depuis plusieurs années sur des révisions taxonomiques d'espèces d'arbres forestiers que l'on trouve en Ethiopie, à Djibouti, et en Somalie et sur la compilation de données de répartition, l'habitat, etc. Ce travail concerne en particulier des espèces qui peuvent atteindre une hauteur de 8 mètres ou plus. L'auteur s'interesse tout particulièrement aux espèces présumées endémiques. Environ 200 espèces correspondent à ce critère. L'auteur a préparé des cartes de répartition des espèces et est en train de préparer des analyses phytogéographiques des éléments divers de la flore d'arbres forestiers.

The forests of Ethiopia and Somalia have until recently been poorly known. Very little forest was recorded by the early travelers in northern Ethiopia, e.g., by W. G. Schimper in Tigre, Semien, and Begemder, although he collected a considerable number of specimens of forest trees, presumably from free standing individuals left in deforested country or from ravine forests. Early travelers in southern Ethiopia (e.g., O. Neumann and F. Bieber) reported on vast expanses of rain forest in southwestern Ethiopia, which it was only possible to penetrate by cutting one's way (Engler, 1906: 746–747). Unfortunately, these early collectors made very few collections from the forest regions.

Until about 1945, the botanical collections from, and the literature about, the forests in Ethiopia and Somalia were mainly due to the activity of Italian expeditions, individual collectors, or foresters in official capacity (with an exception of northern Somalia). The main work on the forests of Eritrea is by Fiori (1912), in which he accounted for his own collections and those made by G. Schweinfurth, D. Riva, A. Terracciano, and A. Pappi. The main collectors in southern Somalia were G. Paoli, G. Stefanini, N. Puccioni, and others, whose collections have been published by Chiovenda (1916, 1929, 1932, 1936, 1940). The forests in particular were dealt with by Senni (1935), who both accounted for his own collections and those of others. In Ethiopia, Chiovenda (1912), Cufodontis et al. (1939), Pichi-Sermolli (1951), and a number of foresters including Giordano (1939–1940) and Senni (1940) are among the chief contributors to the knowledge of the forests. The important 19th century expedition of E. Ruspoli and D. Riva covered both parts of Somalia and Ethiopia, and collected important forest specimens from southern Ethiopia, as did several other expeditions by travelers of various nationalities. An important British contribution was the collec-

[1] I should like to acknowledge the help of my colleagues and companions on field trips in Ethiopia: Asfaw Hunde, Getachew Aweke, M. G. Gilbert, the late K. Jakobsen, Mesfin Tadesse, K. Vollesen, and Zerihun Woldu. Also Tewolde Berhan G. Egziabher and Zemede Asfaw have been of great help during the fieldwork. The Carlsberg Foundation, the Danish Natural Science Research Council, and the Ethiopian Flora Project (% Prof. O. Hedberg and Tewolde Berhan G. Egziabher) have supported the fieldwork and other travel. M. G. Gilbert, J. B. Gillett, G. Moggi, C. Puff, B. Verdcourt, K. Vollesen, and F. White have kindly helped with taxonomic problems or have taken the trouble to discuss other botanical matters in relation to this project. My wife, Victoria C. Friis, has read and criticized the present text.

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tions of Gillett (1941), who worked both in eastern Ethiopia and British Somalia.

A brief summary, with special emphasis on forest trees of southwestern Ethiopia, was produced by Logan (1946), and the entire literature on the vegetation of Ethiopia, Djibouti, and Somalia was surveyed by Pichi-Sermolli (1957) for his vegetation map of the region.

During the 1960s traveling in Ethiopia was greatly facilitated by the construction of new roads. In the 1950s through the 1970s, more than 30 botanical collectors from Ethiopia, Europe, and the United States, including J. Ash, W. Burger, I. Friis, M. G. Gilbert, O. Hedberg, W. Kuls, Mesfin Tadesse, F. G. Meyer, H. F. Mooney, R. M. Perdue, F. Rasmussen, O. Sebald, Tewolde Berhan G. Egziabher, M. Thulin, K. Vollesen, J. J. F. E. de Wilde, and W. J. J. O. de Wilde, collected in the forests of Ethiopia. A survey of the floristic knowledge of the forests of southwestern Ethiopia was published by Friis et al. (1982), mainly based on their own collections. The material collected by the staff of the Land Resources Development Center of the British Ministry of Overseas Development was published by Chaffey (1979).

Knowledge of the forests of Somalia has not progressed as fast and there is a considerable risk that they will have disappeared before their floristic content is established. Recent collections in forest vegetation in southern Somalia have been made by Gillett, Beckett and White, and by Thulin and Warfa. Reports on these collections have just begun to make their way into the literature.

The Forests: Extension and Classification

The forests of Ethiopia, Djibouti, and Somalia now consist of many small, scattered patches. Only in southwestern Ethiopia and on the southern slopes of the Bale Mountains are there larger expanses of continuous forest. The past range of the Ethiopian forest is not known with certainty, but a reasonable estimate can perhaps be made from maps showing the distribution of the important species, which are often left standing in pastures and farmland or preserved in ravine forests. The original range of the Somalian forests is also unknown, but here the destruction is often complete and there are few old records on which to base an estimate of past distribution.

The forests belong to a variety of types, which are here classified according to the scheme used by White (1983) for the UNESCO/AETFAT *Vegetation Map of Africa.*

In Ethiopia, the composition of forests varies with the great differences in rainfall, altitude, and substrate which exist within the country. In western Illubabor, at altitudes between 500 and 600 m, there is a comparatively dry type of forest which floristically seems to belong with White's drier peripheral semi-evergreen Guineo–Congolian rain forest and similar forest in the transition zones. On the southwestern escarpment of Kaffa, Illubabor, and Wollega there are types of more humid forest with strong West African floristic affinities. These forests should probably also be classified with the lowland type mentioned above.

In the Ethiopian highlands there is a range of Afromontane forest types, from Afromontane rain forest in southern Wollega, in Illubabor, Kaffa, Gemu-Gofa, Sidamo, and Bale, through undifferentiated Afromontane forest in the central Ethiopian region to single-dominant Afromontane forest (*Juniperus procera* forest) in the northern, eastern, and southern parts of the plateau. The Dai Forest, the only forested area in Djibouti, should be included in the latter.

On the long mountain range in northern Somalia, the eastern escarpment of the Ethiopian plateau, and the slope between the Ethiopian highlands and the extensive plains in southern Somalia, there are patches of single-dominant Afromontane forest (*Juniperus procera* forest), with a transition to East African evergreen and semi-evergreen bushland and thicket, with occasional tree species reaching above the canopy of shrubs. The distinction between forest and bushland can be quite difficult in these areas.

In southern Somalia there are patches of Zanzibar–Inhambane undifferentiated forest and Zanzibar–Inhambane scrub forest. Riverine forest occurs along rivers throughout both Ethiopia and Somalia, but tends to have discontinuous canopy along the nonpermanent streams ("tugs") in northeastern Somalia, which makes a clear definition of riverine forest in that area difficult to use.

The Project

My first fieldwork in the forests of southwestern Ethiopia was carried out in 1970 and 1972–1973. After 1975 I did not have opportunity to travel in Ethiopia for some years, and I therefore

looked for a wider context in which the results of the first two periods of fieldwork could be used. At that time the published data about the forests of Ethiopia in general and the humid southwestern forests in particular was rather limited, as it will appear from statements by Pichi-Sermolli (1957: 82) about the Afromontane rain forests of southwestern Ethiopia: "Le nostre conoscenze sulla costituzione dei consorzi di questa foresta sono molto superficiali," and from White (1970: 110) about the Ethiopian forests at large: "The forests of Ethiopia are still very imperfectly known . . . ."

On the other hand, a considerable number of botanical specimens had accumulated in the herbaria of Europe and Africa during the 1950s, the 1960s, and the early 1970s, and this material could be utilized for an atlas project of the forest flora. My idea for such a project was influenced by the AETFAT meeting in Geneva in 1974, especially by the papers of White (1976a, 1976b). At the Geneva meeting it was concluded that the existing herbarium specimens in European and African herbaria would generally be adequate for the preparation of distribution maps of ecologically important species.

At the same meeting Moggi (1976) presented a new estimate of the degree of floristic exploration of Ethiopia, Djibouti, and Somalia. This estimate was based on a survey of the distribution maps published in the first 30 families (17 pteridophytes, 13 angiosperms) contributed to the *Adumbratio Florae Aethiopicae*. The study showed that there were specimens from Ethiopia and Somalia in at least 38 herbaria but also that by far the largest amount of the material was concentrated at Kew (K) and Florence (FT). This would make it possible to record the larger amount of all existing specimens from Ethiopian forests.

From the map published with Moggi's paper, it appeared that certain parts of interest to the mapping of forest species were well explored, especially areas on the central Ethiopian plateau and in Eritrea. In addition, areas along the major roads in other parts of Ethiopia and the major rivers in Somalia, the upper zones of the higher mountains in Ethiopia, and the peaks in the mountain range in northern Somalia were fairly well collected. From the point of view of mapping forest species, the entire fringe of western lowlands of Ethiopia, the western highlands of Gojjam, Wollega, Illubabor, and Kaffa, and large parts of Bale were very poorly known. The inland areas of southern Somalia were also poorly known.

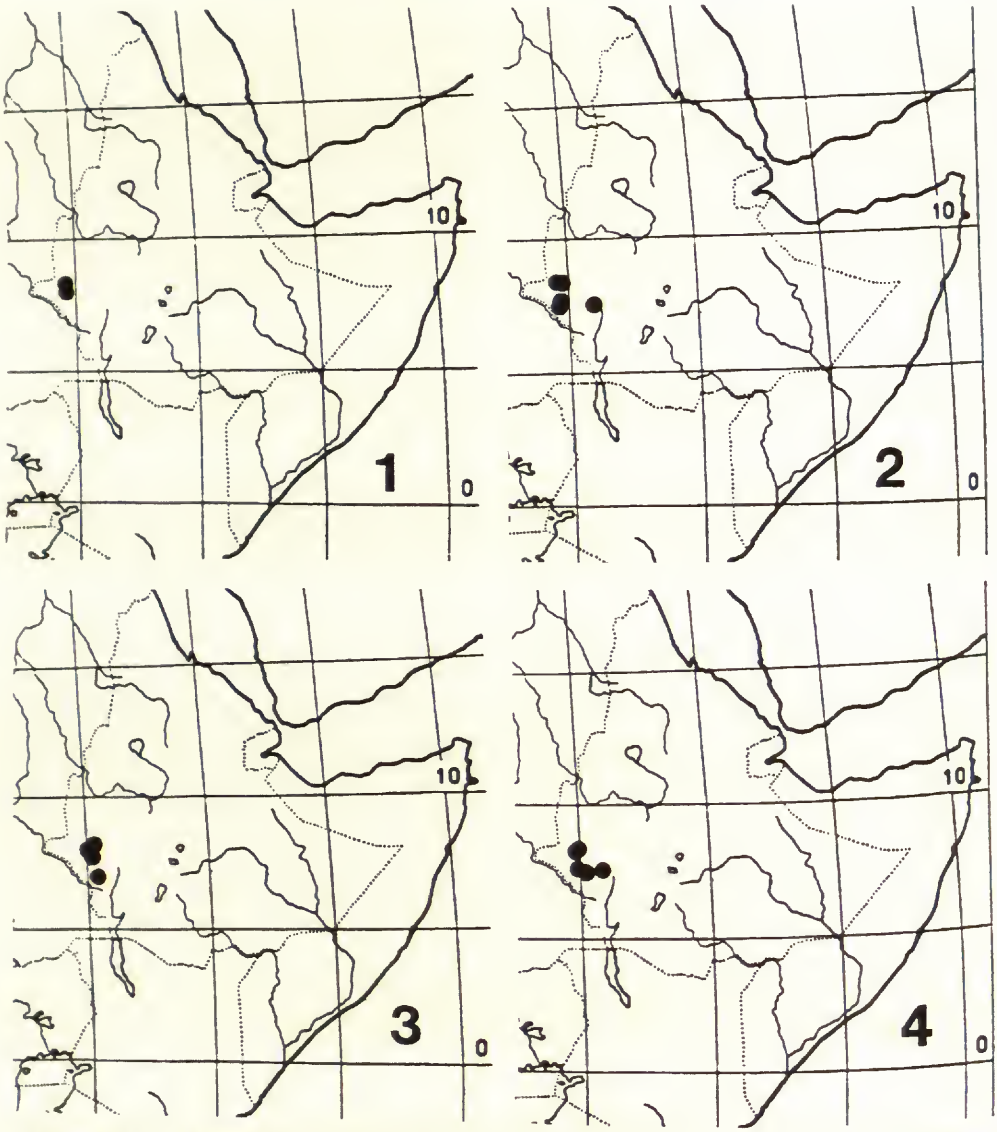
In these latter areas, collections made since 1976 have added to the knowledge of the forests of western Illubabor and Kaffa (both in the highlands and the lowlands), Bale, and southern Somalia. Information from western Gojjam and Wollega is still very scarce and it is suspected that virtually unexplored patches of forest exist near or on the western escarpment in these regions (Gilbert, pers. comm.).

Even if the latest collections are included, distribution maps of widespread forest species prepared from herbarium material still show some disjunctions that are difficult to believe. Often distribution maps of widespread species reflect the patterns formed by the Ethiopian roads. However, I believed the results obtained so far encouraging enough to have proceeded with the project, and the maps obtained meet the requirements of White (1976a) reasonably well.

Which taxa would it then be feasible to include in an atlas of forest plants? The best known and taxonomically best studied species would be the trees. Maps of forest trees would, as suggested in the section about the composition of the forests, perhaps be of some help in the estimation of the former extent of forests of the region. The maps would probably also be of help in identifying ecologically important tree species and perhaps make possible a floristically based subdivision of the forests. This might eventually help to characterize units in future vegetation maps of the region. I therefore decided to concentrate on producing distribution maps of the forest trees.

Having decided to map forest trees, I was faced with three problems: 1) how to define the term "forest," 2) how to define the term "tree," and 3) how to obtain a list of names of species that meet the former two definitions from the study area. The two first questions do not have absolute answers, and I therefore decided to accept the definitions of White (1970). This meant the exclusion of species that have not been reported to reach a height of 8 m or more. The third question meant careful search in field notes of collectors and in herbaria and literature, in order to make sure that the list was reasonably complete.

The project would necessitate taxonomic revisions of a number of species of forest trees, especially all the assumed endemics. It would also require compilation of information about distribution and ecological amplitude from herbaria in western Europe and Africa from as many

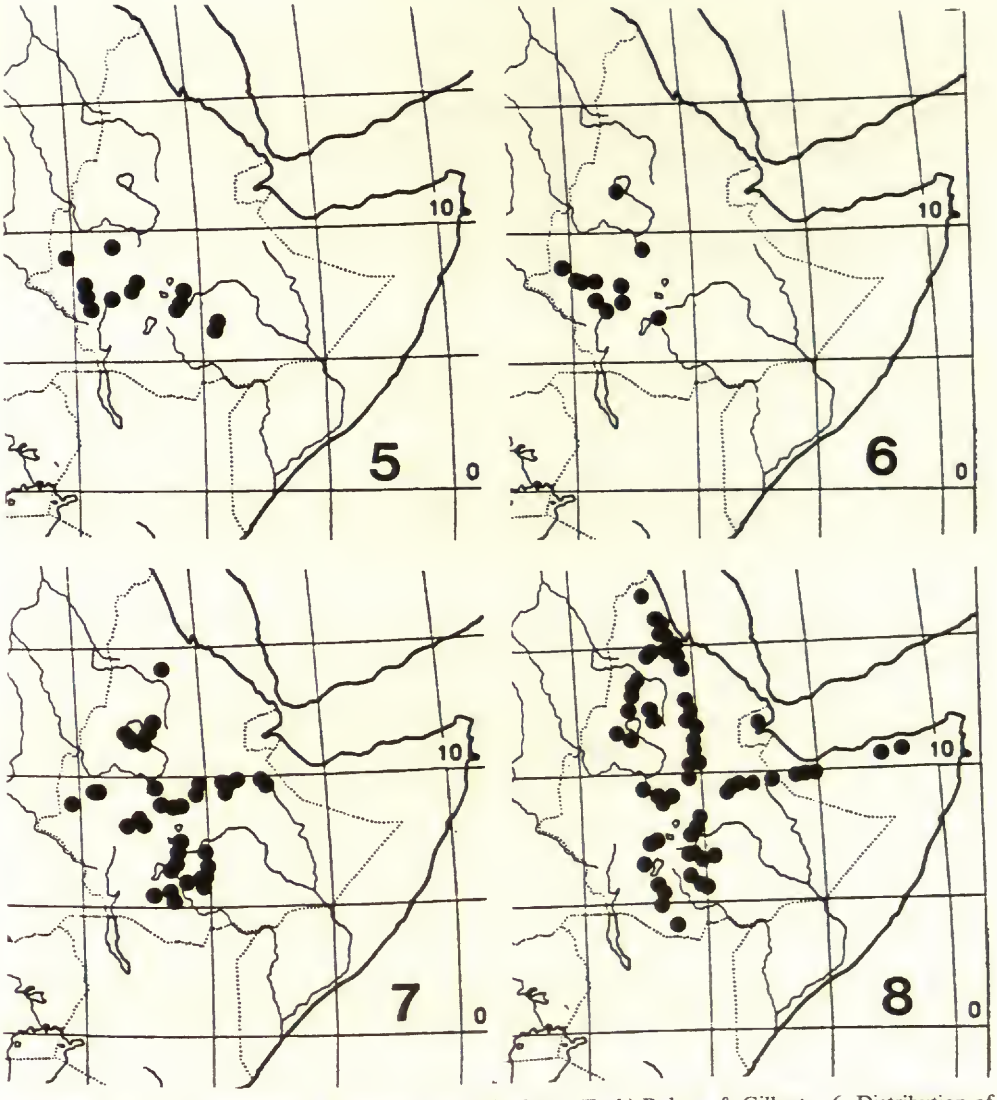


FIGURES 1–4.—1. Distribution of *Trichilia prieuriana* A. Juss. (Meliaceae).—2. Distribution of *Trilepisium madagascariense* A. DC. (Moraceae).—3. Distribution of *Mitragyna rubrostipulata* Havil. (Rubiaceae).—4. Distribution of *Elaeodendron buchananii* (Loess.) Loess. (Celastraceae). (Distributions in Sudan, Uganda, and Kenya are not shown.)

as possible of the 38 herbaria reported by Moggi (1976) to have material of Ethiopian and Somalian plants.

As a consequence of this, data were assembled on index cards from specimens in herbaria in Belgium (BR), Britain (BM, K, FHO), Denmark (C), Ethiopia (ETH), France (P, ALF), Italy (FT), Kenya (EA), Netherlands (WAG), Sweden (S, UPS), and U.S.A. (US). At first I intended to include forest trees from Ethiopia only, but the project was later enlarged to include also forests of Djibouti and Somalia. The inclusion of Djibouti and northern Somalia was a natural step, as the mountains of Ethiopia and northern Somalia form a natural continuum, also from a phytogeographical point of view (Figs. 8, 11, 12).

What I should do with the forest trees of southern Somalia was less obvious. This doubt was

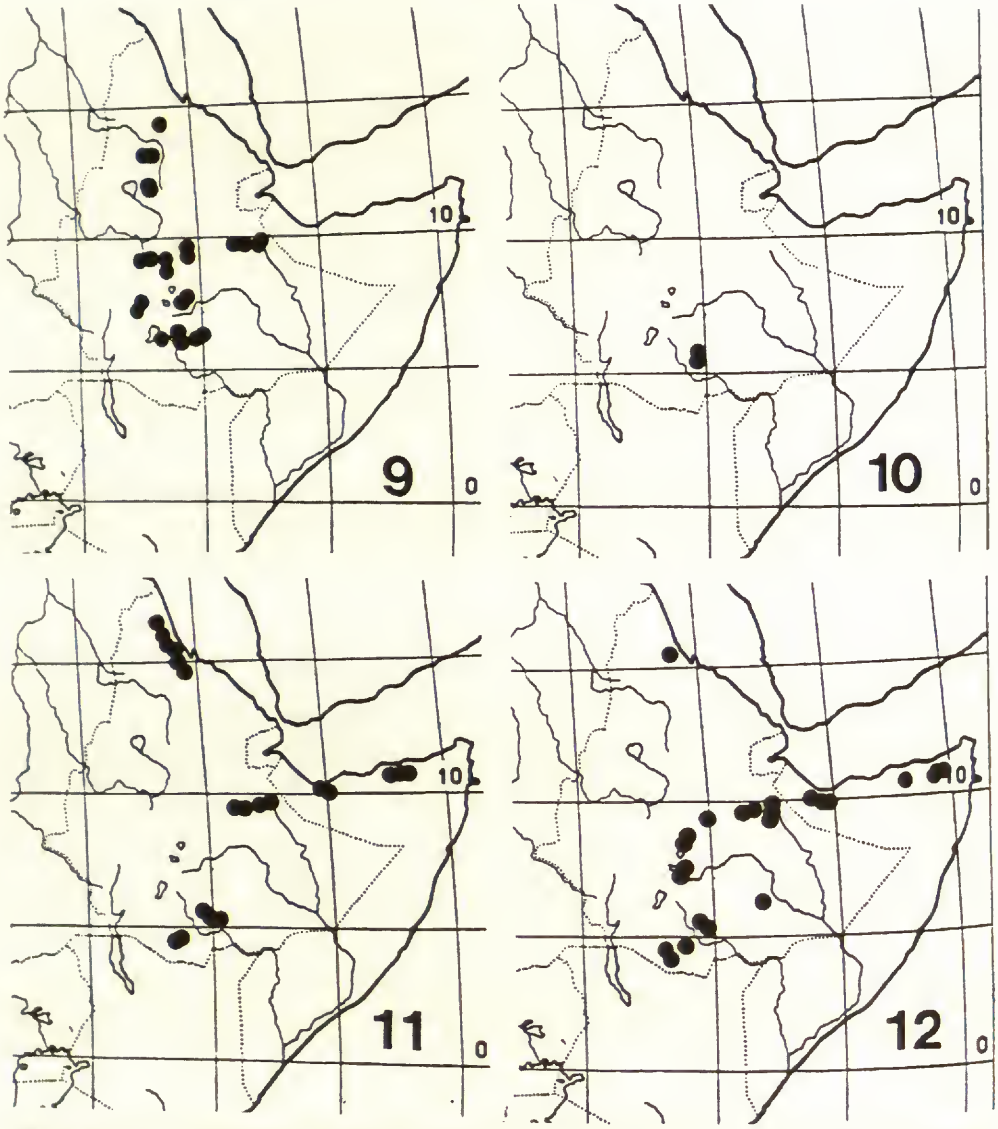


FIGURES 5–8.—5. Distribution of *Aningeria adolfi-friedericii* (Engl.) Robyns & Gilbert.—6. Distribution of *Rothmannia urcelliformis* (Hiern) Robyns (Rubiaceae).—7. Distribution of *Podocarpus gracilior* Pilger (Podocarpaceae).—8. Distribution of *Juniperus procera* Endl. (Cupressaceae). (Distributions in Sudan, Uganda, Kenya, Yemen, and Saudi Arabia are not shown.)

partly caused by phytogeographical reasons, as the floristic overlap between the forests of Ethiopia–northern Somalia on one hand and of southern Somalia on the other (apart from the riverine forests) is minimal (Figs. 13, 14), and the forests of southern Somalia are floristically more closely related to the coastal forests of Kenya. But it was also caused by the rather restricted knowledge of the forests of southern Somalia.

Almost all the material available for mapping the forest trees of southern Somalia was available in Florence (FT), where considerable material necessary for mapping the forest trees of Ethiopia was also found. Therefore, I decided to include southern Somalia in the project.

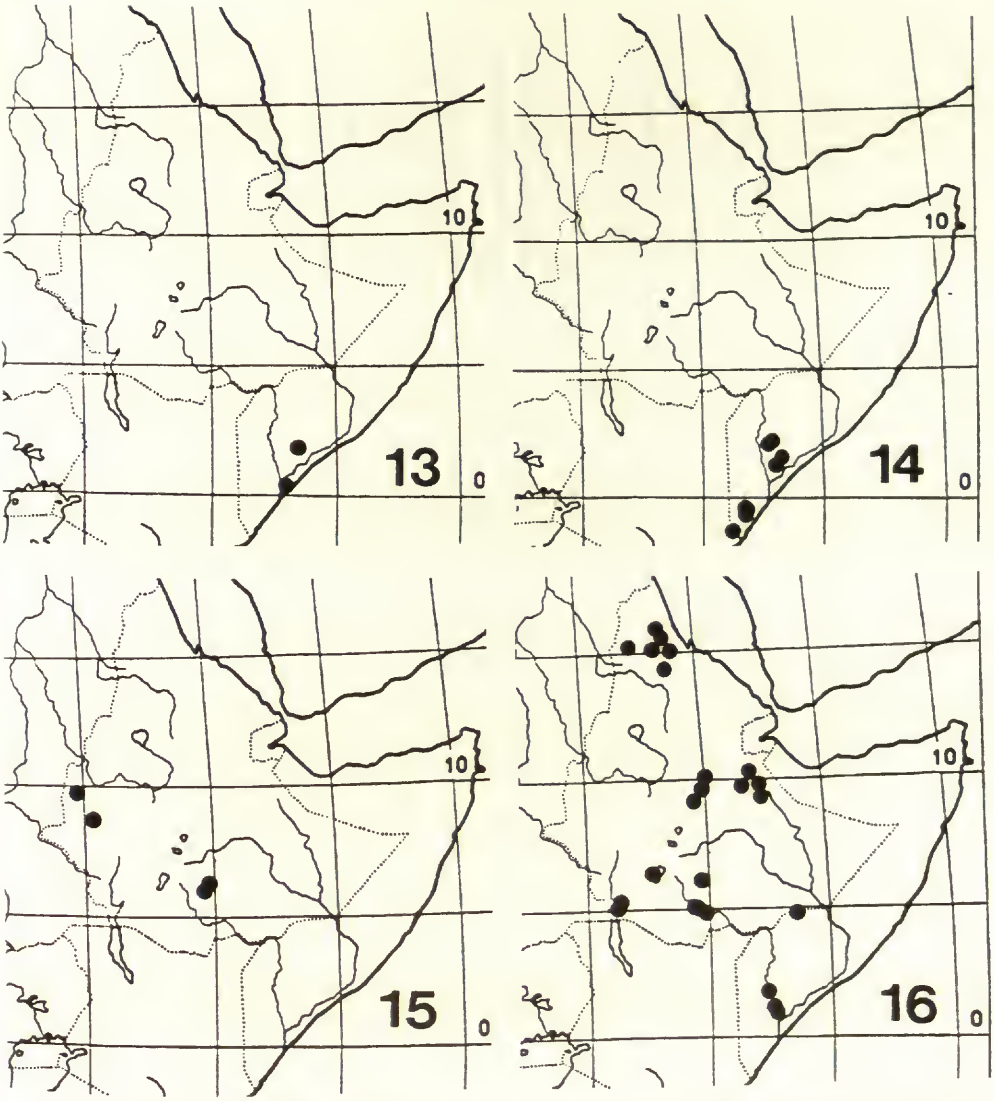
The inclusion of southern Somalia has considerably increased the work with taxonomic revisions, as a number of species have been described



FIGURES 9–12.—9. Distribution of *Hagenia abyssinica* J. F. Gmel. (Rosaceae).—10. Distribution of *Felicium decipiens* (Wight & Arn.) Thwaites. (Sapindaceae).—11. Distribution of *Barbeya oleoides* Schweinf. (Barbeyaceae).—12. Distribution of *Cussonia holstii* Engl. (Araliaceae). (Distributions in Sudan, Uganda, Kenya, and Yemen are not shown.)

as endemic from that area, especially by Chiovenda in *Flora Somala* (Chiovenda, 1929, 1932, 1936). The majority of these studies have now been published or are in the course of publication (see below). The Rubiaceous flora of the south Somalian forests is being studied by Bridson in connection with the preparation of her account for the *Flora of Tropical East Africa*. This has also led to the identification of a number of supposed endemic forest trees [e.g., *Randia ravae* Chiov. as *Rothmannia r.* (Chiov. Bridson) (Bridson, 1984)].

During field trips in 1982 and 1984 (both in connection with the Ethiopian Flora Project), I was able to visit additional forest types in Ethiopia, but unfortunately I have still no field experience with the forests of southern Somalia and have had to base my interpretations on the lit-



FIGURES 13–16.—13. Distribution of *Ficus scassellatii* Pamp. (Moraceae).—14. Distribution of *Croton megalocarpoides* Friis & M. G. Gilbert (Euphorbiaceae).—15. Distribution of *Breonadia salicina* (Forssk.) Hepper & Wood (Syn. *Adina microcephala* (Del.) Hiern; Rubiaceae).—16. Distribution of *Trichilia emetica* Vahl. (Meliaceae). (Distributions in Sudan, Uganda, Kenya, and Yemen are not shown.)

erature, personal information from collectors (chiefly J. B. Gillett and M. Thulin), and on short visits to presumably floristically related forest types in adjacent Kenya.

RESULTS

The project has resulted in a list of tree species, the identity of which has been verified either by checking specimens from the study area against modern taxonomic revisions, monographs, and material identified by authors of such papers, or by original research (Friis, 1978, 1981a, 1981b, 1984a, 1984b, 1985a, 1985b, 1985c; Friis & Gilbert, 1984; Friis & Vollesen, 1981, 1985). For some groups, the start of the Ethiopian Flora Project in 1980–1981 has been of considerable help.

TABLE 1. A survey of data on the 16 samples of tropical northeast African forest trees.

Figure	Species	Family	Altitudinal Range	Occur in Study Area in Forest Type
1	*Trichilia prieuriana* A. Juss.	Meliaceae	550–700 m	Drier peripheral semi-evergreen Guineo–Congolean rain forest and similar forest in the transition zones (White, 1983: 79), drier lowland type.
2	*Trilepisium madagascariense* DC. syn. *Bosqueia phoberos* Baill.	Moraceae	800–1,800 m	Drier peripheral semi-evergreen Guineo–Congolean rain forest and similar forest in the transition zones (White, 1983: 79), wetter type of the escarpment; marginally intruding into Afromontane rain forest (White, 1983: 164).
3	*Mitragyna rubrostipulata* Havil.	Rubiaceae	1,800–2,050 m	Wettest type of Afromontane rain forest (White, 1983: 164).
4	*Elaeodendron buchananii* (Loes.) Loes.	Celastraceae	1,000–1,300 m	Margins of wetter type of Afromontane rain forest (White, 1983: 164); this is surprising, as the species further south in Africa is associated with drier montane forest (White, pers. comm.).
5	*Aningeria adolfi-friedericii* (Engl.) Robyns and Gilbert.	Sapotaceae	1,300–2,450 m	Throughout the Afromontane rain forest (White, 1983: 164), of which it is one of the most characteristic species in the study area.
6	*Rothmannia urcelliformis* (Hiern) Robyns	Rubiaceae	950–2,100 m	In wetter types of Afromontane rain forest (White, 1983: 164); the overall distribution of the species indicates that it is a marginal intruder from Guineo–Congolian rain forest, but it has not yet been found in the drier lowland types of this category in Ethiopia or Somalia.
7	*Podocarpus gracilior* Pilger	Podocarpaceae	1,500–2,800 m	Throughout the presumed former area of undifferentiated Afromontane forest (White, 1983: 165) in Ethiopia.
8	*Juniperus procera* Endl.	Cupressaceae	1,100–3,100 m	In drier types of undifferentiated Afromontane forest and dominant in single-dominant Afromontane forest (White, 1983: 165), also in the transition between the latter type and the East African evergreen and semi-evergreen bushland and thicket (White, 1983: 115).

TABLE 1. Continued.

Figure	Species	Family	Altitudinal Range	Occur in Study Area in Forest Type
9	*Hagenia abyssinica* (Bruce) J. F. Gmel.	Rosaceae	1,850–3,400 m	In the upper zones of undifferentiated Afromontane forest and dominant in single-dominant Afromontane forest (White, 1983: 165–166).
10	*Filicium decipiens* (Wight and Arn.) Thwaites	Sapindaceae	1,600–1,800 m	In the lower zones of undifferentiated Afromontane forest (White, 1983: 165), probably a marginal intruder.
11	*Barbeya oleoides* Schweinf.	Barbeyaceae	1,200–2,500 m	Associated with forest, scrub, and woodland in the transition between single-dominant Afromontane forest (*Juniperus procera* forest) and the East African evergreen and semi-evergreen bushland and thicket (White, 1983: 115).
12	*Cussonia holstii* Engl.	Araliaceae	1,500–2,600 m	Associated with forest, scrub, and woodland in the transition between single-dominant Afromontane forest (*Juniperus procera* forest) and the East African evergreen and semi-evergreen bushland and thicket (White, 1983: 115).
13	*Ficus scassellatii* Pamp.	Moraceae	?100–300 m	? Riverine forest, or Zanzibar–Inhambane undifferentiated forest (White, 1983: 187).
14	*Croton megalocarpoides* Friis and M. G. Gilbert	Euphorbiaceae	25–400 m	Probably Zanzibar–Inhambane undifferentiated forest (White, 1983: 187).
15	*Breonadia salicina* (Vahl) Hepper and Wood syn. *B. microcephala* (Del.) Ridsdl., *Adina microcephala* (Del.) Hiern	Rubiaceae	1,000–1,200 m	Riverine forest; seems restricted to this forest type throughout its distributional range.
16	*Trichilia emetica* Vahl.	Meliaceae	100–1,850 m	Riverine forest; elsewhere also in riparian woodland.

So far the list includes about 200 species, the majority of which have been mapped. Information for each species has been compiled from field observations, literature, or herbarium labels about altitudinal range, range of habitat, including rainfall regimes, and distribution in the study area and overall distribution.

All species have been assigned to local distribution type (within the study area), which is usually a reflection of local ecological conditions. Most species have also been assigned to phytogeographical element according to their overall distribution. The classification of phytogeographical elements is basically derived from the works of White (1970, 1983). An analysis of the local distribution types and the phytogeographical elements is being carried out. A small part of the material has been utilized in connection with a previous paper on the mountain flora of Ethiopia and Somalia (Friis, 1983). However, I plan to publish the whole study in a monographic account.

A sample of the distribution maps of 16 species has been included here (Figs. 1–16) in order to demonstrate how selected species are distributed in the study area. Information on the 16 species is given in Table 1.

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DISTRIBUTION OF SUBFAMILIES AND TRIBES OF POACEAE IN SOUTHERN AFRICA[1]

G. E. Gibbs Russell[2]

Abstract

All five subfamilies of Poaceae occur naturally in southern Africa with three of them—Panicoideae, Chloridoideae, and Arundinoideae—each predominant in a major climatic region: panicoids in summer rainfall areas with over 500–600 mm of rain, chloridoids in more arid summer rainfall areas, and arundinoids in areas with more than 40% winter rainfall. Pooideae and Bambusoideae are of more restricted occurrence. Indigenous pooids form a major component of the grass flora only at high altitudes, and exotic pooids are a major component of the grass flora along the south and southwest Cape coast. The bambusoid grasses are represented by very few taxa, never form a major component of the grass flora, and are restricted to high rainfall areas and isolated wet habitats. Within the largest subfamilies, some tribes show differences in distribution pattern and attain their greatest concentration of species outside the area where their subfamily is the major component of the grass flora, which is the area of greatest overlap in the distribution of the constituent tribes. Analysis of distributions at the scale of degree grids was made possible for the first time by the production of checklists for each grid, based on 60,000 grass specimens for southern Africa from the Pretoria National Herbarium Computerized Information System (PRECIS). The results at this fine scale agree with world trends in grass distributions reported by previous researchers for congruence of climate and habitat with the conditions of greatest efficiency for the pathways C_3 and C_4 photosynthetic.

Résumé

Les cinq sous-familles des Poacées au complet sont autochtones dans le sud de l'Afrique et trois d'entre elles—les Panicoidées, Chloridoidées, et Arundinoidées—prédominent chacune dans une zone climatique importante: les Panicoïdées dans des régions où il pleut surtout l'été (avec plus de 500–600 mm de pluie), les Chloridoïdées dans des régions où il pleut également l'été mais plus arides, et les Arundinoïdées dans des régions avec plus de 40% de pluvoisité hivernale. Les Pooïdées et les Bambusoidées appraissent dans des endroits plus restreints. Les pooidées indigènes forment un composant important de la flore gramioïde seulement à haute altitude et pour les pooïdées exotiques le long des côtes sud et sud-ouest du Cap. Les Bambusoïdées ne sont représentées que par quelques taxons et ne forment jamais un composant important de la flore graminoïde. Elles sont restreintes au régions à la pluvoisité forte et aux habitats humides isolés dans les localités arides. Les tribus comprises dans les plus grandes sous-familles ont des shémas de répartition differents. Certaines tribus ont leur plus forte concentration d'espèces en dehors de la région où leur sous-famille représente le composant majeur de la flore graminoïde, celle-ci est donc la région où il y a le plus de chevauchement dans la répartition des tribus qui la composent. L'analyse des répartitions à l'échelle d'un degré de latitude et de longitude fut possible pour la premiere fois grâce à la préparation d'une liste pour chaque secteur, basée sur 60.000 échantillons de Graminées pour le sud de l'Afrique du Pretoria National Herbarium Computerized Information System (PRECIS). Les résultats à cette échelle correspondent aux tendances mondiales dans les répartitions graminoïdes qui avaient été décrites précédémment par des études antérieures sur la congruence de climat et d'habitat avec les conditions de meilleure efficacité pour les types de photosynthèse C_3 et C_4.

Subfamily classification in the Poaceae has been based on cryptic characters since the work of Avdulow (1931), which led to the realignment of the two previously accepted subfamilies defined on spikelet morphology into several groups defined by cytological and anatomical criteria. Since that time, a number of authors have put forward variations and refinements based on differing sets of characters, the most recent being that of Renvoize (1981), whose classification of grasses into five subfamilies is based on leaf anatomy alone. Many of these anatomical characters indicate the photosynthetic pathway, and a single pathway predominates in each of the subfamilies and tribes. The two photosynthetic pathways found in grasses differ in the climatic conditions under which they operate most efficiently. The C_3 pathway, common to most angiosperms, is efficient under relatively cool conditions and lack of water stress. The C_4 pathway, which the Poaceae alone of plant families has exploited through many species, is efficient under conditions of high

[1] I am grateful to W. Roux, who prepared all the maps, and R. P. Ellis and R. H. Westfall for much discussion.
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TABLE 1. Number of taxa in Poaceae for southern Africa. Poaceae is the seventh largest family in the flora.

Taxon	Number
Subfamilies	5
Tribes	24
Genera	200
Species and infraspecific taxa	962

light intensity and high temperature and confers tolerance of low moisture conditions (Bjorkman, 1976). The C_4 pathway has two basic variants, malate formers and aspartate formers, named for the carbon fixation product. Aspartate formers are further subdivided into PEP-ck (phosphoenolpyruvate carboxykinase) species and NAD-ME (NAD-malic enzyme) species on the basis of enzyme differences (Ellis, 1977).

Hartley (1950, 1958a, 1958b, 1961, 1973) and Hartley & Slater (1960) showed worldwide distribution patterns of panicoid, chloridoid, and pooid grasses based on percentage occurrence in different areas. Cross (1980) analyzed distribution patterns for all five subfamilies in the Old World on the basis of species numbers. The region where each subfamily or tribe forms the largest percentage of the flora, or where it has a concentration of species, coincides with climatic conditions where its photosynthetic pathway is most efficient. Clayton (1981, 1983) has combined this information into a succinct account of the physiology and worldwide distribution of each subfamily.

In the southern hemisphere of the Old World, distributions of grass taxa of the C_3 and C_4 photosynthetic pathways have been shown by Vogel et al. (1978) and Ellis et al. (1980) for southern Africa, and more recently by Hattersley (1983) for Australia. Their results agree with the now-familiar pattern of cool mesic growing seasons for C_3 grasses and warm mesic to arid conditions for C_4 grasses. However, so far these studies have not been linked to subfamily distributions.

The aim of this study is to show for southern Africa the areas where the different subfamilies and tribes predominate and to correlate these areas with climatic conditions. Because the classification system is then related to the distribution through the physiology of the plants, the predictive power of subfamily and tribal classification in the Poaceae is demonstrated and made available for practical application. This follows the example of Hartley (1963), who made recommendations for introduction of pasture plants to Australia on an empirical basis, without the detailed knowledge of photosynthetic physiology that has been determined in the intervening two decades.

TABLE 2. Comparison of the number of species and infraspecific taxa in each subfamily of Poaceae for southern Africa.

Subfamily	Number of Taxa	% of Total Taxa	Number of Naturalized Taxa	% of Taxa in Subfamilies That Are Naturalized
Bambusoideae	13	1	3	23
Arundinoideae	236	24	3	1
Chloridoideae	232	24	11	5
Panicoideae	339	35	22	6
Pooideae	142	15	67	47

METHODS

The National Herbarium Computerized Information System (PRECIS) records distribution data for the more than 600,000 herbarium specimens from southern Africa in the National Herbarium, Pretoria (PRE) (Gibbs Russell, 1985). About 62,000 grass specimens have their locality expressed as a quarter degree grid reference, and these specimens were sorted by computer to give a checklist for each of the nearly 3,900 quarter degree grids that cover southern Africa. However, it was not feasible to analyze the distributions at that very fine scale because the collecting intensity for southern Africa, as shown by PRECIS, is grossly uneven. There are many more specimens from the mesic eastern and southern regions than there are for the arid central and western regions, where fewer than 10 specimens are recorded for over two-thirds of the quarter degree grids (Gibbs Russell et al., 1984). In order to overcome this problem, distributions were analyzed at the level of whole degree grid. Quarter degree grid checklists were combined to give a checklist for each whole degree grid. In general, degree grid checklists with fewer than 20 grass taxa were omitted from the study. In arid areas where the known species diversity is low and where the checklist presented

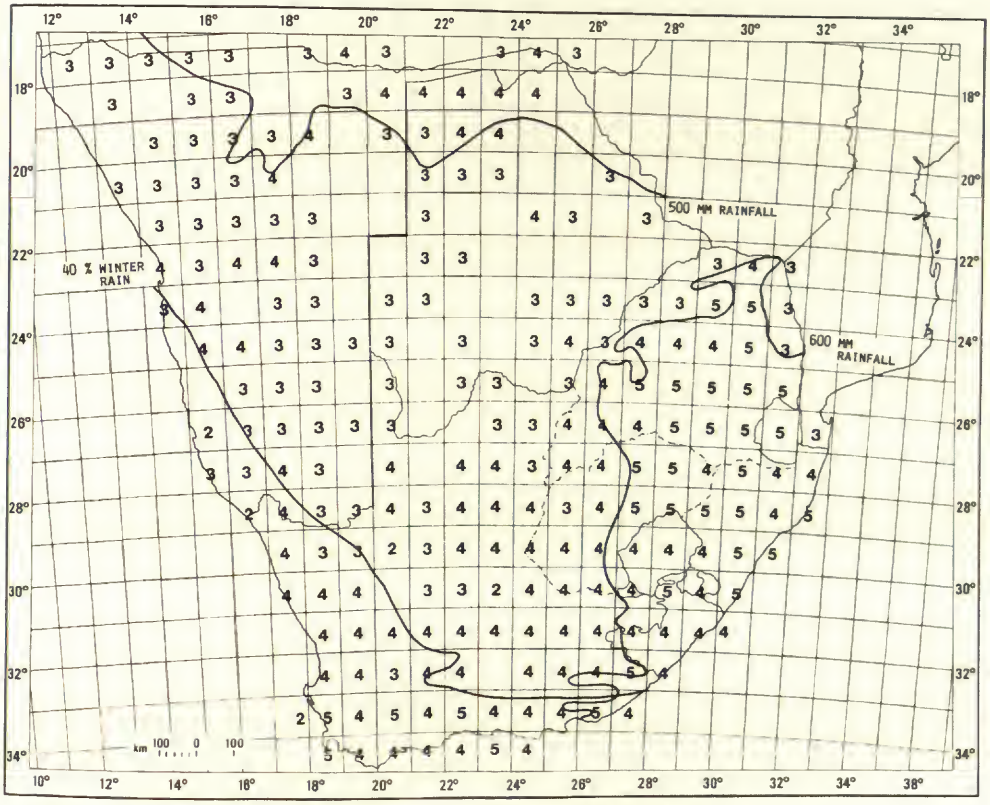

FIGURE 1. Number of subfamilies of Poaceae recorded for each degree grid.

a clear pattern, a few degree grids with less than 20 taxa were included. Of the 256 whole and partial degree grids in southern Africa, only 39, all from arid regions, were insufficiently collected for the purposes of this study; therefore, these results represent 85% of the total area. Because of the known 7% error load in PRECIS for correct names on specimens and correct grid references, questionable taxon distributions appearing on the checklists were verified in the herbarium.

Studies of plant distributions can be based either on percentage occurrence, such as those of Hartley (1950, 1958a, 1958b, 1961, 1973), Vogel et al. (1978), and Ellis et al. (1980), or on absolute numbers of taxa, such as those of Clayton & Hepper (1974), Clayton (1975, 1976), and Cross (1980). Only Hattersley (1983) has used both percentages and species numbers and explained the differences implied by the two methods. In order to use species numbers for comparison, it is necessary to have reliably complete checklists for each area subdivision. The variation in collection records shown by PRECIS indicates that for many of the undercollected degree grids the species lists are in fact not complete. Therefore, in this study the distributions are reported on the basis of the percentage of taxa in each grid that represent each of the subfamilies or tribes.

RESULTS AND DISCUSSION

The numbers of grass taxa occurring in southern Africa are shown in Tables 1 and 2. The species and infraspecific taxa and the naturalized taxa are not evenly distributed among the five subfamilies. Over a third of the taxa are panicoids, and the chloridoids and arundinoids each comprise about a fourth of the taxa. Thus, nearly 85% of the taxa occur in only three of the subfamilies, and in these subfamilies the percentage of naturalized species is low. The two smaller subfamilies, Bambusoideae and Pooideae, have a higher percentage of naturalized species. In the Pooideae nearly half the taxa are naturalized, and nearly two-thirds of all naturalized species are members of this subfamily.

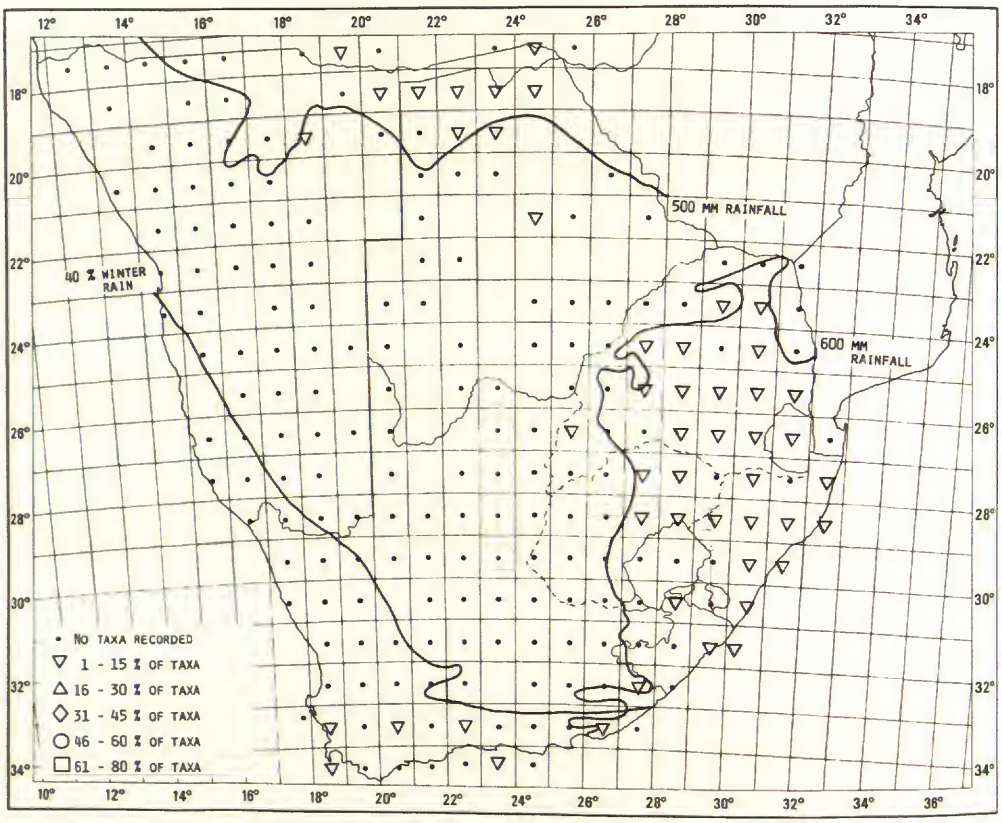

FIGURE 2. Distribution of the subfamily Bambusoideae (13 taxa, 1% of grass flora).

The number of subfamilies recorded for each of the degree grids is illustrated in Figure 1. In the mesic summer rainfall areas there are commonly five subfamilies, and in the drier areas there are often only three subfamilies present. However, since overall collecting intensity has been shown to be greatest in the mesic areas, it may be that the presence of all five subfamilies in mesic areas reflects collecting intensity rather than the real distribution of subfamilies: perhaps fewer subfamilies are reported for the hot dry areas because they are undercollected. Analysis of the distribution of each of the subfamilies given below shows that the distribution of each is consistent with the photosynthetic pathways of its constituent tribes and genera. The C_3 Bambusoideae and Pooideae are generally absent from warmer and more arid areas. Furthermore, Hattersley (1983) reports for Australia that the number of species of both C_3 and C_4 grasses is greatest in the wetter parts of the continent. The presence of more grass taxa in the wetter parts of southern Africa is consistent with these results. Within this overall pattern of subfamily abundance, I have examined the distribution of taxa in each of the subfamilies.

BAMBUSOIDEAE

The Bambusoideae (Fig. 2) form a very small proportion of the southern African grass flora, and the subfamily never comprises more than 10% of the taxa (three or four species at most) in any degree grid. The species are limited to mesic areas in the eastern and southern regions and to wet habitats in the arid areas. The tribes Bambuseae (two indigenous species) and Olyreae (one species, probably introduced) occur in forested localities from the eastern Transvaal south to Natal, Transkei, and the eastern Cape. In the tribe Oryzeae the two aquatic genera, *Oryza* and *Leersia*, are the only bambusoids that occur outside the mesic areas. The third genus, *Prosphytochloa*, is also a forest grass and has the same distribution as the true bamboos. The particularly low number of bambusoids, which are typ-

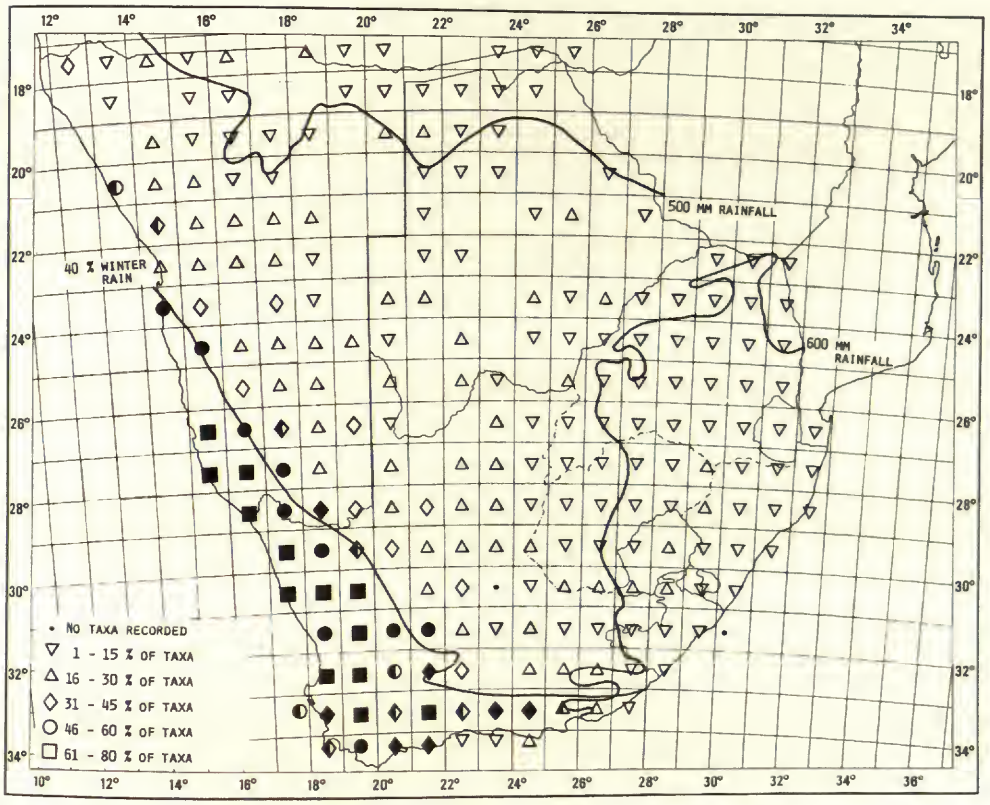

FIGURE 3. Distribution of the subfamily Arundinoideae (236 taxa, 24% of grass flora). Shaded symbols indicate degree grids where the subfamily comprises the largest percentage of the grass flora.

ically forest-dwelling, is another example of depauperization in the African flora resulting from fluctuations in forest area following Quaternary climatic changes discussed by Brenan (1978). The restriction of the Bambusoideae to forest and aquatic habitats is consistent with the C_3 photosynthetic pathway exhibited by all the species.

ARUNDINOIDEAE

The Arundinoideae (Fig. 3) form the largest percentage of the grass flora in degree grids with more than 40% winter rainfall, and the subfamily is present in virtually all degree grids. Most of the taxa are C_3 and the cool conditions during the spring growing season in the area where they have their greatest diversity is consistent with the conditions of greatest efficiency of the C_3 photosynthetic pathway. However, not all the arundinoids are C_3 grasses. Of the four tribes, only Ehrharteae (35 taxa) and Centosteceae (1 taxon) are completely C_3; Arundineae is predominantly C_3 (120 C_3 taxa and 2 C_4 taxa); but Aristideae is predominantly C_4 (76 C_4 taxa and 2 C_3 taxa).

The tribe Ehrharteae reaches its highest percentage among the arundinoids in the degree grids with more than 40% winter rainfall. Only two species occur in summer rainfall areas, one as a weed in the central and northern Cape and one as a forest grass from the eastern Cape northward through Natal and the Transvaal to Ethiopia. The single species in the tribe Centosteceae is also a forest grass occurring in Natal. The tribe Arundineae also reaches its highest percentage of taxa per degree grid in the winter rainfall area south of the Orange River, and the high percentages extend into the summer rainfall regions eastward in the mountains of the eastern Cape, Lesotho, and Natal. This tribe occurs at very low percentages in scattered degree grids in the hotter and drier parts of the summer rainfall area. It is most commonly represented in these areas by the widespread aquatic C_3 genus *Phragmites*, the semiaquatic tropical C_3 genus *Elytrophorus*, and

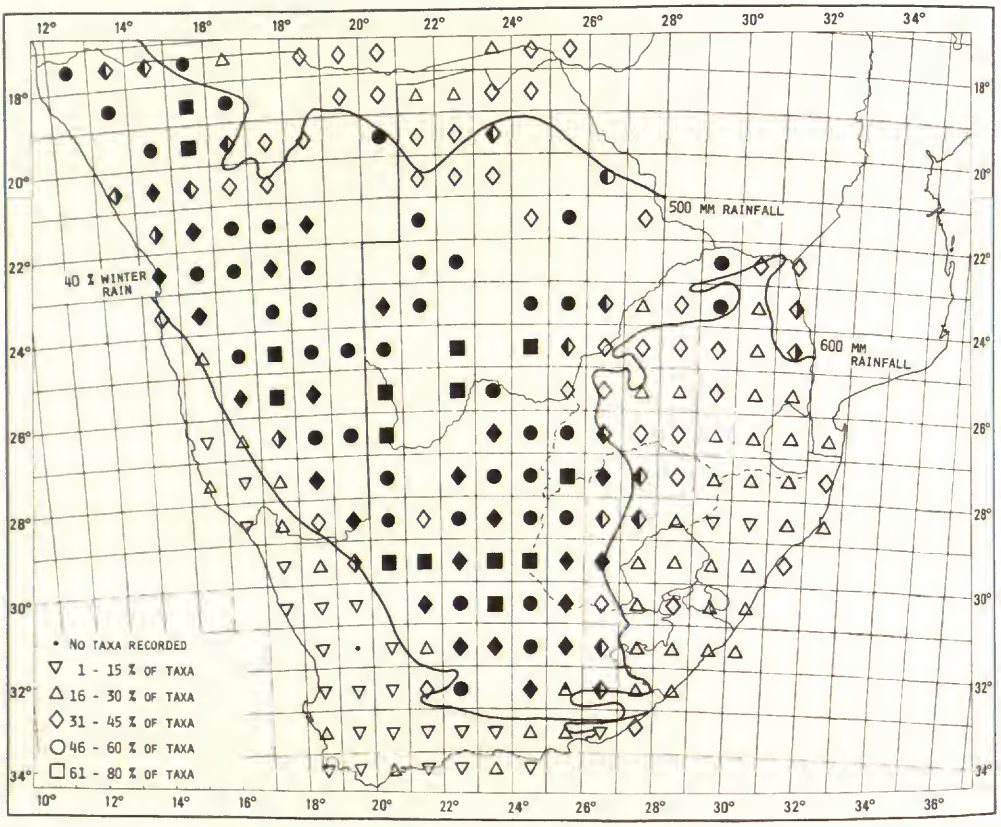

FIGURE 4. Distribution of the subfamily Chloridoideae (232 taxa, 24% of grass flora). Shaded symbols indicate degree grids where the subfamily comprises the largest percentage of the grass flora.

the single C_4 genus in Arundineae, *Asthenatherum*. The predominantly C_4 tribe Aristideae shows a different pattern from the C_3 tribes. It forms the highest percentage of arundinoids in the summer rainfall degree grids where *Aristida* and *Stipagrostis* are usually the only arundinoids present. The tribe is present at a low percentage in virtually all degree grids. The rare C_3 genus *Sartidia* occurs in a few high-altitude localities in the tropics.

The distribution of tribes within the subfamily reflects the areas and habitats where conditions are most favorable for the different photosynthetic types, with Ehrharteae (C_3) being concentrated in winter rainfall areas, Arundineae (predominantly C_3) being concentrated in winter rainfall and high altitude areas outside the tropics, and Aristideae (predominantly C_4) being concentrated in summer rainfall and tropical areas. The exceptional taxa within each tribe tend to follow a distribution pattern related to the photosynthetic pathway rather than to the distribution of the majority of taxa in the tribe. The C_3 taxa occurring in the summer rainfall areas (e.g., *Phragmites, Elytrophorus, Ehrharta erecta* Lam., *Megastachya mucronata* (Poir.) Beauv., *Sartidia jucunda* (Schweick.) De Winter) are found either at high altitudes, in forests, or in aquatic habitats. Conversely, C_4 taxa occurring in this predominantly C_3 subfamily (e.g., Aristideae, *Asthenantherum*) have their distribution centered in the summer rainfall areas rather than the winter rainfall areas characteristic of the tribe.

CHLORIDOIDEAE

The Chloridoideae (Fig. 4) form the largest percent of the grass flora in summer rainfall areas with less than 600 mm of rain outside the tropics and less than 500 mm of rain in tropical regions. Chloridoid taxa are reported from all degree grids except one, but are least numerous and form the

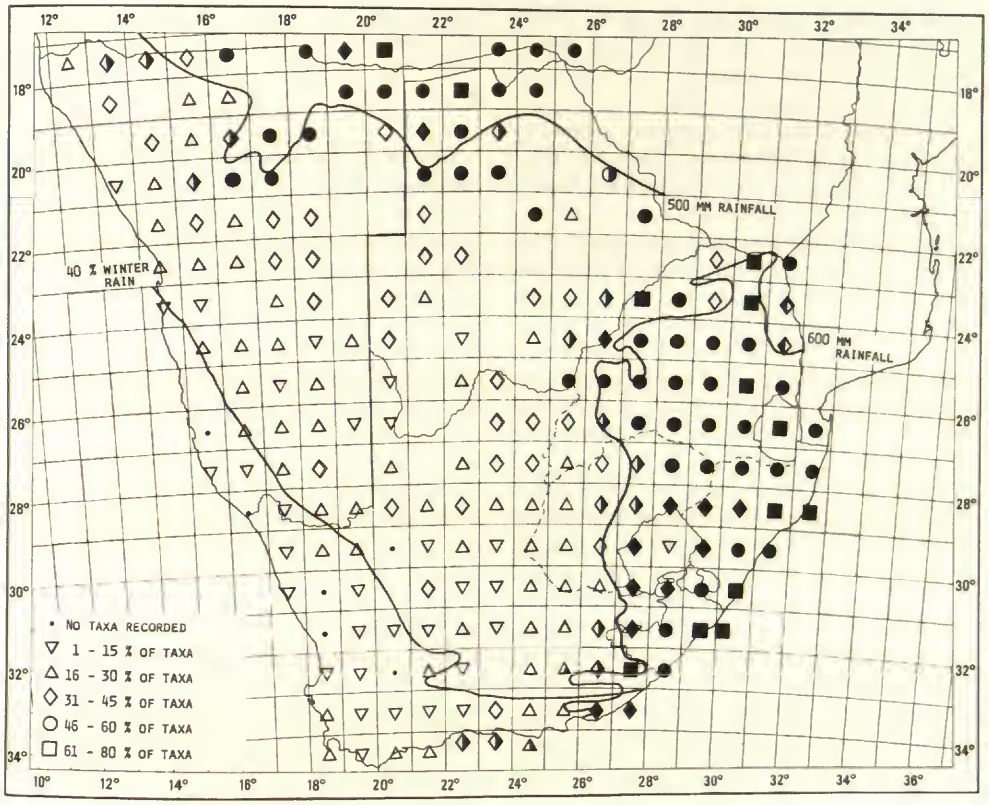

FIGURE 5. Distribution of the subfamily Panicoideae (339 taxa, 35% of grass flora). Shaded symbols indicate degree grids where the subfamily comprises the largest percentage of the grass flora.

smallest percentage of the grass flora in the winter rainfall areas of the southwestern Cape. Within this basic pattern there appears to be little difference in the distribution patterns of the four tribes Pappophoreae, Eragrostideae, Cynodonteae, and Leptureae. All the taxa are C_4 aspartate formers (Ellis, 1977) except for one species, *Eragrostis walteri* of the Namib desert, which has recently been shown to have C_3 leaf anatomy (Ellis, 1984). This species, like other C_3 summer rainfall taxa discussed above, is restricted to aquatic habitats. Two other C_3 species that occur with it are the only representatives of their respective subfamilies found in these habitats.

Ellis et al. (1980) showed that among the C_4 grasses in South West Africa/Namibia, the C_4 aspartate forming taxa comprised the largest percentage of the grass flora in the most arid regions, while the C_4 malate formers were more abundant in mesic regions. These results can now be extended to include the summer rainfall regions of all southern Africa and be interpreted at the subfamily level when comparing the distribution of the Chloridoideae and Panicoideae (Fig. 5). The chloridoids are all C_4 aspartate formers, and they make up the largest percentage of the grass flora in low-rainfall regions, whereas the panicoids are predominantly C_4 malate formers (51 out of 64 genera reported by Ellis (1977)), and they make up the largest percentage of the grass flora in high-rainfall regions.

PANICOIDEAE

The Panicoideae (Fig. 5) form the largest percentage of the grass flora in summer rainfall areas with more than 600 mm of rain outside the tropics and 500 mm of rain in tropical regions. The degree grids in the northwestern Transvaal and eastern Botswana that connect these two rainfall zones also have a majority of panicoid species. Like the chloridoids, the panicoids reach their

lowest percentage of the grass flora in the winter rainfall areas of the southwestern and northwestern Cape, and six degree grids in this region have no panicoid taxa reported.

Panicoideae is the only subfamily in the Poaceae with C_3 and all three variations of C_4 photosynthetic pathways. Two of the tribes, Andropogoneae and Arundinelleae, are strictly C_4 malate formers, but the third and largest tribe, Paniceae, exhibits the entire range of photosynthetic pathways found in the grasses. Six genera have C_3 taxa, 11 genera have taxa with C_4 malate forming photosynthesis, and 11 genera have taxa with C_4 aspartate forming photosynthesis. Of the C_4 aspartate formers, all 11 genera have PEP-ck taxa, and 2 of the genera have NAD-ME taxa (Ellis, 1977).

Distribution of the tribes reflect these differences in photosynthesis. Andropogoneae, whose taxa are all C_4 malate formers, reaches its highest percentage of the panicoids in summer rainfall areas with over 500 mm of rain, but Paniceae, whose genera are evenly divided between C_4 malate formers and C_4 aspartate formers, reaches its highest percentage of the panicoids in summer rainfall areas with less than 500 mm of rain. Both tribes are present in all degree grids in the high-rainfall areas, but in regions with less than 500 mm of rain, Paniceae is absent from only 3 degree grids, all in the northwestern Cape, whereas Andropogoneae is absent from 38 degree grids scattered throughout the arid regions. The small tribe Arundinelleae has only C_4 malate forming taxa. It reaches a high percentage of the Panicoideae in only one degree grid in the northeastern Transvaal but is present at low percentages in most degree grids with more than 500 mm of summer rainfall. The tribe occurs in only scattered degree grids in arid areas, most of these in the northcentral part of Namibia. These tribal distribution patterns again confirm the findings of Ellis et al. (1980) that C_4 malate formers show higher occurrence in mesic areas and C_4 aspartate formers predominate in arid areas.

The C_3 taxa in the tribe Paniceae inhabit as usual a cooler or more mesic "C_3 habitat" in the summer rainfall areas. *Acroceras* and *Sacciolepis* are aquatic plants, and *Oplismenus, Pseudechinolaena,* and the C_3 species of *Panicum* are forest grasses. Only one C_3 taxon, *Alloteropsis semialata* (R. Br.) Hitch. subsp. *eckloniana* (Nees) Gibbs Russell, occurs in open grasslands, but its range extends farther to the south and it grows at higher altitudes than the closely related C_4 taxon *A. semialata* subsp. *semialata* (Gibbs Russell, 1983).

POOIDEAE

The Pooideae (Fig. 6), like the other C_3 subfamily Bambusoideae, has comparatively fewer taxa and is of more restricted distribution in southern Africa than the three larger subfamilies that include C_4 taxa. Furthermore, nearly half the pooid taxa are naturalized aliens (Table 2), and have been part of the southern African flora only since the coming of European man. The indigenous pooids form the largest percentage of the grass flora in the single degree grid that covers the high mountains of Lesotho. In addition, indigenous pooids form a major component of the grass flora, along with other subfamilies, in the high altitude degree grids of Somerset East in the eastern Cape and Sutherland in the southwestern Cape. Naturalized pooids, along with other subfamilies, form a major component of the grass flora in four coastal degree grids in the winter rainfall area. The subfamily is absent from the northernmost parts of the area and is reported from only one degree grid north of the tropic of Capricorn. In arid areas it is represented by four species, all of which are annual weeds that grow by ephemeral water bodies. The occurrence of Pooideae in appreciable numbers only in relatively cool and moist places is in agreement with the optimum conditions for C_3 photosynthesis.

Because of the comparatively large number of tribes with few species in each (indigenous species/tribe ratio = 7.4), tribal distributions have not been separately analyzed in the Pooideae. Instead, the distribution of the naturalized and indigenous taxa in the subfamily has been compared. The distribution of the indigenous pooids is centered in Natal and the southern Transvaal, extending north to the eastern Transvaal and westward across the Karoo. In these degree grids there are more indigenous than naturalized pooid taxa. The naturalized pooids are more abundant than the indigenous taxa in a rough ring around the area where the indigenous taxa are concentrated, extending from the south and southwestern Cape coast northward to Namibia, and eastward through the northern Cape to the northern Transvaal. It appears that there are two different patterns shown here. First, the naturalized pooids are generally weedy in nature and may be expected to be of broader ecological tolerance than

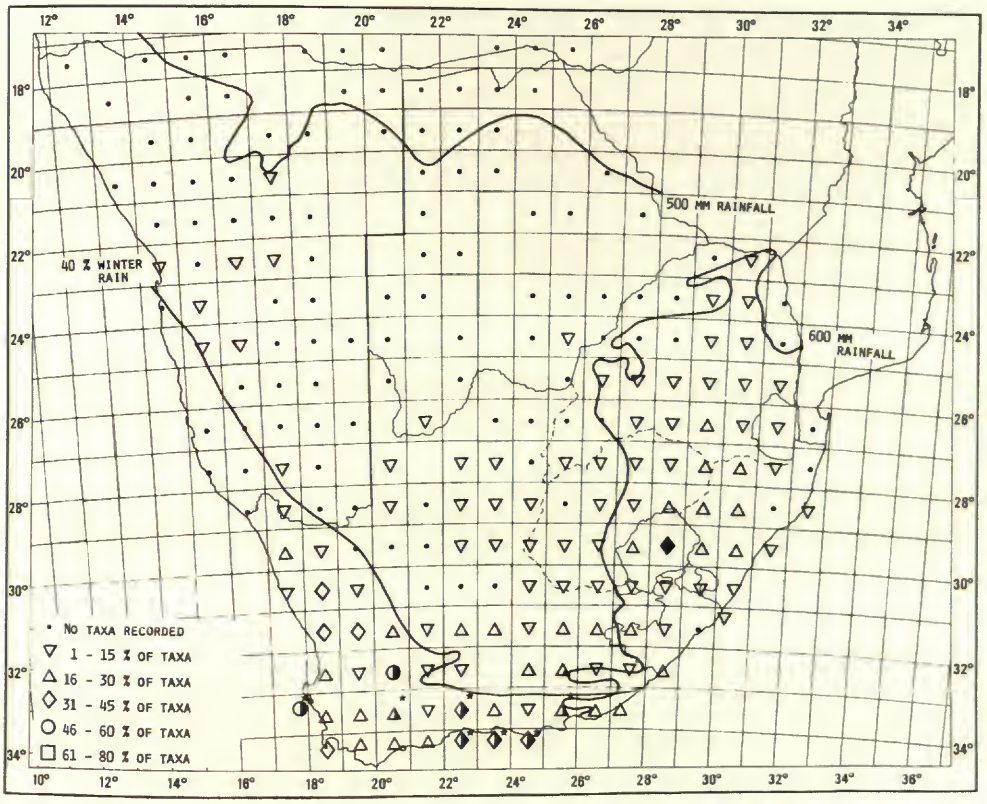

FIGURE 6. Distribution of the subfamily Pooideae (142 taxa, 15% of grass flora). Shaded symbols indicate degree grids where the subfamily comprises the largest percentage of the grass flora. Naturalized taxa are shown by an asterisk.

the indigenous taxa, and thus more successful at the edge of the range in the warmer, drier areas that are normally devoid of C_3 grasses. Second, the concentration of naturalized taxa at the Cape coast may show that this is the port of entry into the continent, and these taxa have not had time to disperse farther inland. However, it may be that because these are C_3 grasses they are unable to spread farther than the cool mountainous coastal climate.

GRASS SUBFAMILY REGIONS FOR SOUTHERN AFRICA

The distribution of each subfamily has been discussed in detail above. When the separate subfamily distributions are combined into a single map (Fig. 7), it can be seen that the three largest subfamilies are each predominant in a region that can be defined by simple environmental conditions related to their major photosynthetic pathway. Arundinoideae (mainly C_3 taxa) comprise the largest percent of grass taxa in the winter rainfall zone, where grasses mature during the cooler early part of the growing season. The Chloridoideae (mainly C_4 aspartate formers) comprise the largest percentage of grass taxa in the summer rainfall zone with less than 500–600 mm of rain, where conditions are arid and warm during the summer growing season. The Panicoideae (mainly C_4 malate formers) comprise the largest percent of grass taxa in the summer rainfall zone with more than 500–600 mm of rain, where conditions are mesic and warm during the summer growing season. The Pooideae (C_3) are not predominant in any discrete region, but form a large percentage of the grass flora in a few degree grids within other regions at high altitudes or coastal areas, where growing conditions are cooler.

At the boundaries between the subfamily regions, such as between the Arundinoid region

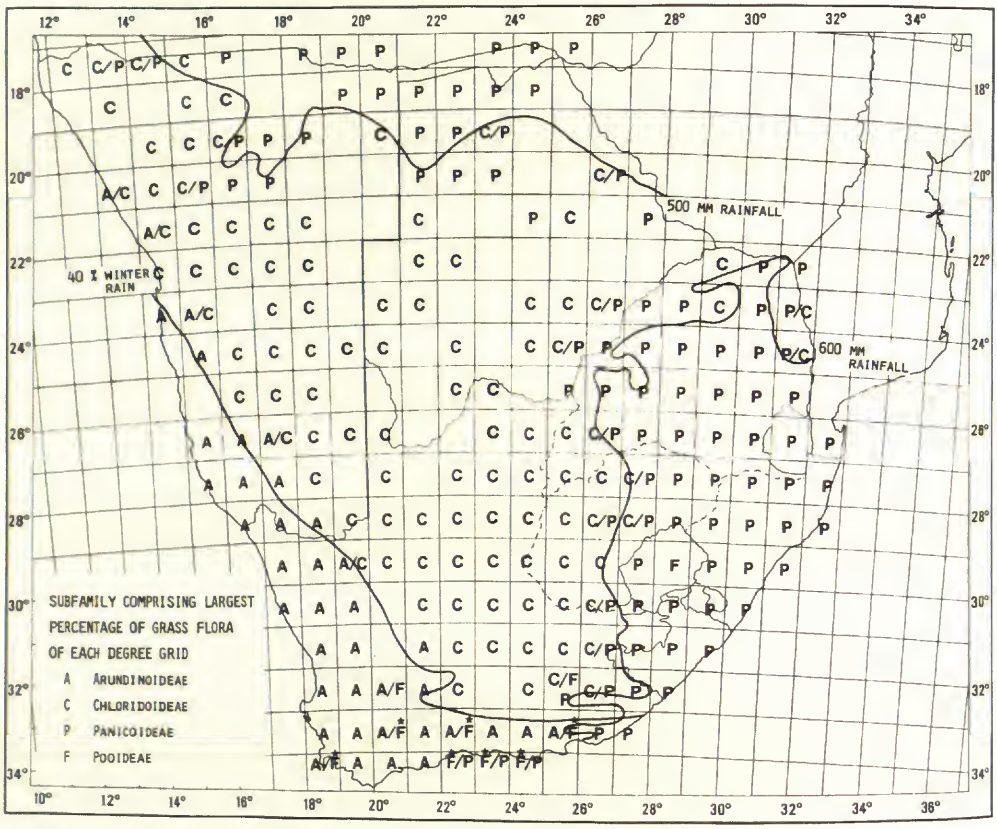

FIGURE 7. Regions in southern Africa where different subfamilies of Poaceae form the largest percentage of the grass flora.

and the Chloridoid region in Namibia, and between the Chloridoid region and the Panicoid region from the eastern Cape to the Transvaal, a number of degree grids have equal percentages of grass taxa in the two subfamilies concerned. The eastern Cape is particularly interesting because the 600 mm rainfall isohyet crosses the winter rainfall zone in this area, and here a number of degree grids have nearly equal representation of different subfamilies. The only degree grid with nearly equal percentages for three subfamilies is in the eastern Cape (Somerset East). Since the eastern Cape is well known to have a wide range of vegetation types and naturalized taxa (Cowling, 1983; Gibbs Russell & Robinson, 1981), the fact that grass subfamily distributions are confused in this area is not unexpected.

The grass subfamily regions, which are determined by percentage of total grass flora, do not coincide with the veld types of Acocks (1975), which are based on differential abundance of a few dominant species. The boundary between the Arundinoid and Chloridoid regions is considerably north and east of his Macchia and Succulent Karoo types, and the boundary between the Chloridoid and Panicoid regions cuts through several of Acocks's Grassveld and Bushveld types. Similarly, the grass subfamily regions also do not correspond to the phytochoria of Werger (1978) and White (1983), which are based on overlapping ranges for many species. The Arundinoid region is much larger than Capensis and smaller than the Karoo–Namib; the boundary between the Chloridoid and Panicoid regions lies through the center of the Zambesian Domain (or Kalahari Highveld Transition Zone); and the Tongaland–Pondoland Regional Mosaic cannot be discerned in the Panicoid region. Only the scattered occurrence of high percentages of indigenous pooids is similar to the divided Afromontane region.

However, the delineation of biomes in southern Africa by correlating life form with environmental factors (Rutherford & Westfall, 1986) has resulted in groupings whose areas correspond to

the grass subfamily regions. The Arundinoid region is roughly equivalent to the Succulent Karoo and Fynbos Biomes, and the boundary between the Chloridoid and Panicoid regions at about 600 mm of rainfall in South Africa is equivalent to the major subdivisions within the Grassland Biome and the Savanna Biome into moist and dry grassland and moist and dry savanna.

Conclusions

1. The distribution of subfamilies and tribes of Poaceae in southern Africa into climatic regions agrees with previous studies of grass distributions in other areas (Hartley, 1950, 1958a, 1958b, 1961, 1973; Cross, 1980; Clayton, 1981).
2. The distribution of taxa with known photosynthetic pathways in southern Africa also agrees with previous studies of environmental conditions correlated with photosynthesis type (Vogel et al., 1978; Ellis et al., 1980; Clayton, 1981; Hattersley, 1983).
3. The grass subfamily regions that summarize the distribution records for individual taxa into environmentally determined areas agree with the division of southern Africa into biomes based on the correlation of plant life forms with environmental factors (Rutherford & Westfall, 1986).
4. PRECIS records for grass distributions have been shown to produce an internally consistent picture that can be interpreted in relation to the physiology of the plants and the environment they inhabit. Therefore, even with its known error load, PRECIS can be accepted as a valid base for biogeographic research.
5. The present distribution patterns for grasses in southern Africa show close agreement with current climatic conditions. Therefore, it can be expected that different climatic conditions would be reflected by different grass distribution patterns. Climatic changes in the past could be demonstrated by differences in grass distributions shown by the pollen record or by carbon isotope ratios in fossil bones of grazing ungulates (Lee Thorp, in press). Climatic changes in the future would result in changes in the proportions of grass subfamilies in particular areas, which would not only affect the plant communities as a whole, but would have significance for the management of natural rangelands that provide the basis for much of agriculture in southern Africa.

These conclusions emphasize the predictive value of a taxonomic classification system. The distribution of subfamilies delimited only by a few cryptic anatomical characters have been shown to coincide with climatic conditions, photosynthetic pathways, and biomes, and can be used to interpret information relevant to disciplines as apparently far removed from classical taxonomy as paleoclimatology, community ecology, and pasture management.

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CLASSICAL TAXONOMY VERSUS MODERN SYSTEMATIC STUDIES IN AFRICAN BOTANY

OLOV HEDBERG[1]

ABSTRACT

Contributions to systematic botany may be roughly sorted into three groups: (1) detailed evolutionary studies, (2) revisions for national or regional floras, and (3) monographic work on a global basis. For most botanists, it will be tempting to make detailed evolutionary studies of small groups, bringing them from α through β toward Ω classification in the sense of Turrill. Such work is intellectually stimulating, academically meritorious, and relatively easy to finance. Revisions for floras are favored by many employers and are therefore usually easily financed, but since the same family is often treated by different botanists for different floras, they usually imply duplication of efforts and variable quality of results. Monographic studies would avoid such difficulties, but since no government feels responsible for the flora of the world, financing is hazardous. Because of the irreplaceable losses of species and genetic diversity caused by the accelerating destruction of tropical ecosystems, it is imperative that we concentrate as much as possible of our taxonomic work on monographic studies by classical methods so as to provide the taxonomic infrastructure required for prudent use of our green heritage on sustained yield basis. Some critical comments on the application of cladistics in systematic botany are included.

RÉSUMÉ

On peut grossièrement classer en trois groupes les contributions à la botanique systématique: (1) des études détaillées de l'évolution, (2) des révisions pour les flores nationales et régionales, et (3) des études monographiques sur une base globale. Pour la plupart des botanistes il est tentant de faire des études évolutionaires détaillées de petits groupes, allant de classifications alpha à des classifications béta puis gamma dans le sens de Turrill. Un tel travail est stimulant sur le plan intellectuel, méritoire d'un point de vue academique, et il est relativement facile à financer. De nombreux employeurs préferent des révisions pour des flores et il est donc habituellement aisé de les financer, mais comme des botanistes différents traitent souvent la même famille pour des flores différentes, il y a en général des répétitions d'efforts et des résultats de qualité variable. Des études monographiques permettraient d'éviter de tels problèmes mais comme aucun gouvernement ne se sent responsable de la flore du monde le financement reste hasardeux. A cause des pertes irremplacables des espèces et de la diversité génétique dûes à la destruction croissante des écosystemes tropicaux il est impératif que nous concentrions autant de travail taxonomique que possible à des études monographiques par des méthodes classiques de manière à fournir l'infrastructure taxonomique requise pour une utilisation prudente de notre héritage végétal sur une base de production continue.

For the AETFAT meeting in Coimbra in 1960, I contributed a paper called "Modern taxonomic methods and the flora of tropical Africa" (Hedberg, 1962). This comes so close to the theme of this eleventh plenary meeting that I felt a reassessment could be worthwhile. I shall therefore briefly survey the purpose of our work, the progress achieved, the succession in research methods employed, and the levels of approach, to conclude with a recommendation on priorities for further studies.

The main tasks of systematic botany are generally agreed to be exploration, description, and classification of the flora of the world. In spite of all the work done by generations of botanists since Linnaeus, these tasks remain incomplete. Approximately 50,000 vascular plant species are undescribed. Because of the accelerated destruction of ecosystems, primarily in the tropics, many of these species will disappear before they can be described. This brings us to a fourth task falling upon systematic botanists, namely conservation—few people are more aware of which plants and ecosystems are in need of conservation than botanical taxonomists, and few others take action about it.

Taxonomic botany, like biology in general, has experienced a succession of partly contemporaneous new approaches or waves of fashion, such as anatomy, serodiagnostics, cytotaxonomy, biosystematics, palynology, phytochemistry, numerical taxonomy, and cladistics. Most of these new approaches were claimed by their proponents to be not only more modern but also more

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scientific than "traditional" systematic botany. Some of these fields were in favor for a relatively short time and then all but disappeared, as serodiagnostics did. Most have persisted for longer periods, although with varying intensity. Not least in the United States, ambitious young botanists have been eager to join the newest wave of research available, whereas the older branches have lost attraction and been left to subside long before their potentials were exhausted. This development has often been accentuated by the attitudes of universities and research councils which have been eager to give priority to the newest approaches at the expense of ongoing research in older but scientifically no less important branches.

Representatives for most of these new approaches have tended to overemphasize the importance of their own pieces of evidence and sometimes attempted to create special classifications that cannot be used for general purpose or for all groups. We have now learned that although each of them can provide a wealth of supporting data, not all pieces of evidence are unequivocal. Most of us will agree that a reliable classification should be based on integration of all pertinent data available, utilizing old methods as well as new.

The two latest approaches, numerical taxonomy and cladistics, stand apart from the others because they do not provide any additional characters, but only concern the manipulation and interpretation of data. Theoretically, numerical taxonomy represents the most objective method of comparing related taxa. But experienced taxonomists are reluctant to attach the same importance to characters known to display interspecific variation as to those known to separate genera. An interesting example of a comparative study using numerical taxonomy and traditional taxonomy on the Jamaican species of *Columnea* and *Alloplectus* has been reported by Stearn (1968). It seems to be generally concluded that whereas numerical taxonomy represents the best approach for microorganisms with few observable features, the classical methods are more likely to provide a reasonable classification for ordinary vascular plants.

The newest wave in systematics is cladistics, which first appeared in the publication *Phylogenetic Systematics* by the German entomologist Willi Hennig (1966). Another pioneer publication is Brundin's (1966) monumental monograph of transantarctic relationships in chironomid midges. Cladistics is claimed by its proponents to be more scientific than Linnean taxonomy and numerical taxonomy because it is phylogenetic (Brundin, 1966: 15). Phylogenetic relationship is judged after (presumed) ancestry: "A species *X* is more closely related to an arbitrary species *Y* than to an arbitrary species *Z* if, and only if, it has at least one ancestor in common with species *Y*, which is not at the same time the ancestor of species *Z*" (Hennig, 1957: 60).

A widespread assumption in cladistic work is that "dichotomy is a general phenomenon in phylogenetic evolution" (Brundin, 1966: 17) and that consequently every group must have a sister group. The definition of sister groups is made in theory after their separation from a common ancestral species but in practice after a number of characters they share, which do not occur in groups considered to be more distantly related.

Fundamental to the theories of cladistics is that the only groups worth discussing are monophyletic groups. "A monophyletic group is one which contains all descendants of a common ancestor" (Humphries & Funk, 1984: 328). Since the ancestry of a species can rarely be traced, cladistics "defines monophyletic groups based on internested sets of synapomorphies" (p. 323). But the determination of synapomorphies is often difficult. The method most often used has been to use outgroups by sampling "a larger group of taxa, which it is hoped contain the sister taxon" (p. 337). In the absence of an identifiable sister group problems are manifold (p. 339). Furthermore, "almost all cladistic studies display a degree of character conflict. These conflicting characters are similarities mistaken to be homologies (false synapomorphies)" (p. 341).

Additional difficulties are caused by hybridization. This is considered to be "a cause of incongruent, intersecting data," which "destroy phyletic information and cause a logical inconsistency in a method designed to present information in hierarchical diagrams" (Humphries & Funk, 1984: 343). This lamentable situation urges me to quote Stebbins's (1950: 28) reminder: "Fickle Dame Nature has very different ends in view from that of creating neat hierarchies of species and genera, which naturalists can file away tidily in cabinets with the least possible trouble."

Part of the explanation for the difficulties met by cladistics is, in my opinion, that the methods are far less objective than has been claimed. Cladistics rests on three basic assumptions: (1) that

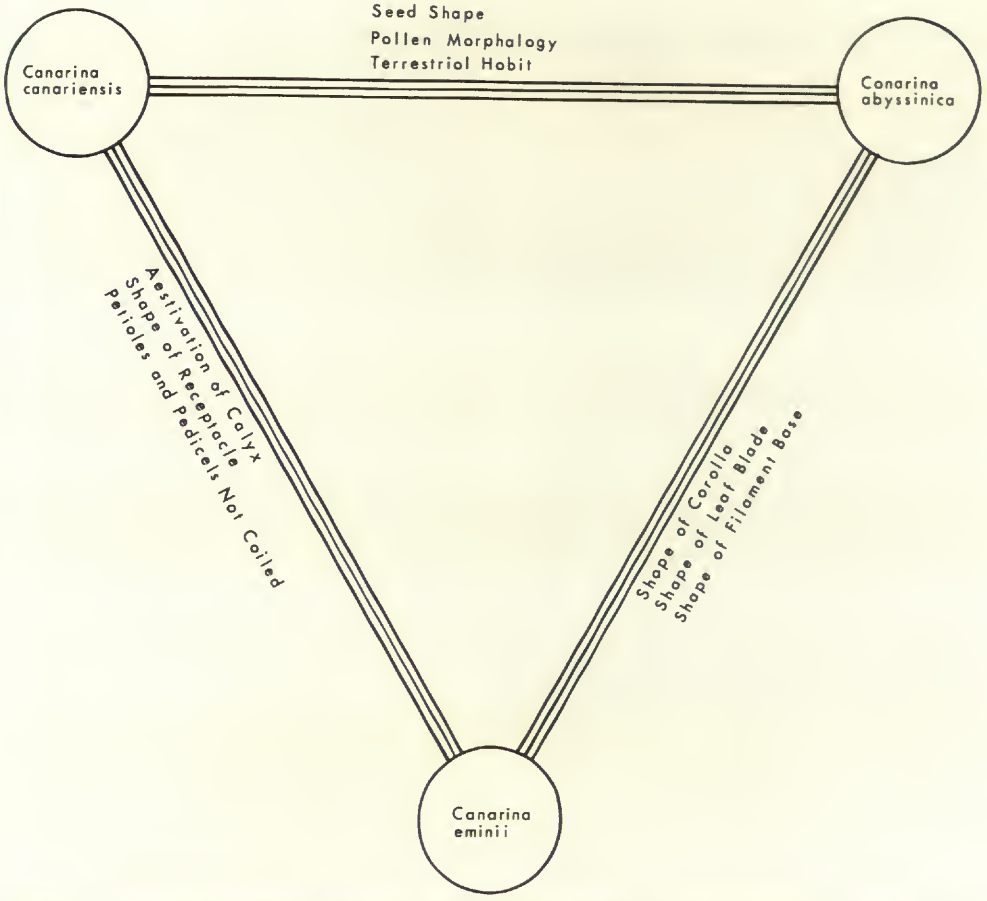

FIGURE 1. Diagram illustrating similarities and differences between the three species of *Canarina*. From Hedberg (1962).

it is possible to define and recognize monophyletic groups, (2) that it is always possible to distinguish between primitive and advanced features—i.e., between plesiomorphies and apomorphies, and (3) that it is possible to distinguish between "true" and "false" synapomorphies. Two more tacit assumptions which seem to lie behind most cladistic schemes are (4) that evolution from primitive to advanced character states normally follows a one-way road without possibilities for reversion, and (5) that differentiation leading to speciation normally involves dichotomy.

As regards monophyly, I am sure most monographers expect their genera to be monophyletic, but this can hardly ever be proved. Who would, for instance, claim *Triticum* to be monophyletic? Whether a character state is primitive or advanced is often difficult to tell. That the conspicuous bracts of the allegedly entomophilous *Fimbristylis* (Cyperaceae) from the West Indies represents a derived state appears plausible (although the whole family might have arisen from entomophilous ancestors), but whether presence of nectaries or absence of perianth in *Salix* are derived characters may be less easy to decide.

Let me take an example on a smaller scale: The genus *Canarina* contains three distinct species (Hedberg, 1961). These share pairwise nine important diagnostic features (Fig. 1). The separation of these into two groups on the basis of "internested sets of apomorphies" seems to me very difficult. Although *C. canariensis* is geographically isolated from the other two, it does not seem to be more distinct from them than they are from each other. Construction of an or-

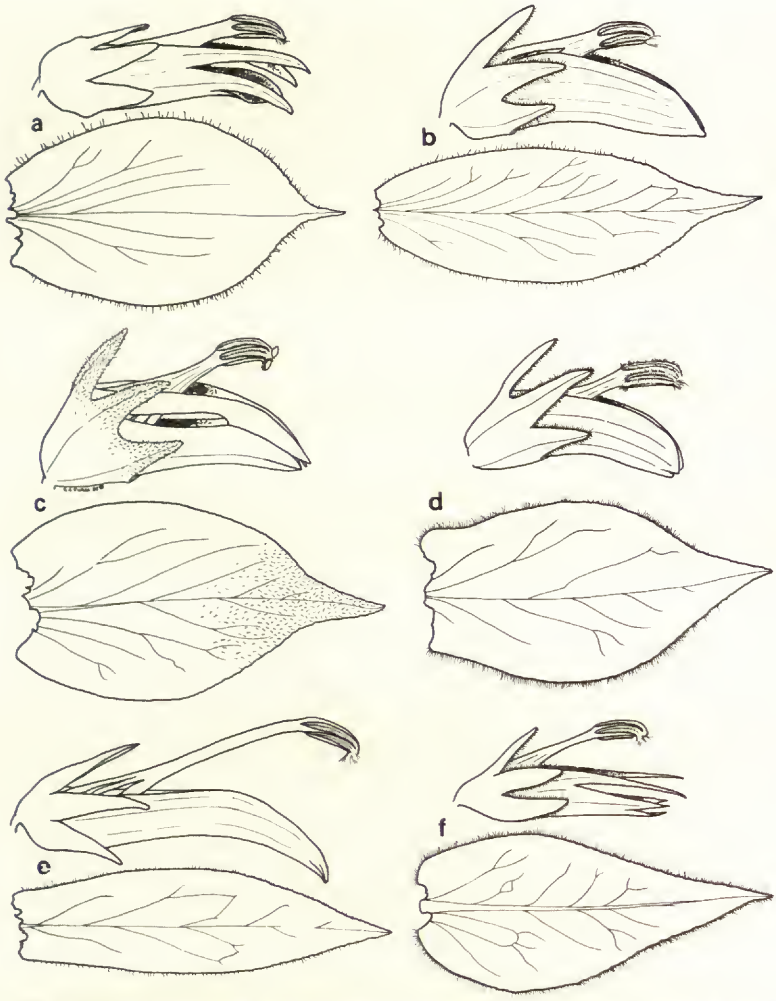

FIGURE 2. Diagram illustrating main morphological difference in flowers and bracts between the six geographically vicarious subspecies of *Lobelia deckenii* (Asch.) Hemsl.—a. ssp. *bequaertii*.—b. ssp. *elgonensis*.—c. ssp. *sattimae*.—d. ssp. *keniensis*.—e. ssp. *deckenii*.—f. ssp. *burtii*. There are also differences in leaf shape and other characters. Magnification ×0.8. Drawing by K. Forss.

thodox cladogram would be no easy matter. Difficulties are of course much worse in larger genera like *Senecio* and *Carex*.

The vast climatic and environmental changes during the Pleistocene must, in many cases, have changed and reversed selection pressures, making evolution deviate from the one-way roads. As regards dichotomy of cladograms and evolutionary paths, I just want to demonstrate one example from East Africa, where there are six vicarious subspecies of a giant *Lobelia* (*L. deckenii*) in six different mountain areas (Fig. 2; Hedberg, 1957; Thulin, 1984). Cases of this sort are probably not uncommon.

As already mentioned, the greatest difficulty for cladistics in botany is caused by hybridization or "reticulate evolution." The difficulty is enhanced by the fact that we don't know enough of its importance. Strictly speaking, hybridization between specimens with dissimilar genotypes is fundamental for evolution. Although it is most common and usually most successful in intraspecific combination, interspecific hybridization is rather common in the flora we see today and often leads to new allopolyploids. Its importance during the evolution of the plant world is not easy to assess, but since most polyploids are likely to be allopolyploids, it appears

FIGURE 3. *Senecio keniodendron* R. E. Fr. & Th. C. E. Fr. Longitudinal section of specimen about 1.7 m tall, terminated by a nyctinastic leaf rosette. In the center of the stem is a thick water-storing pith (gray in the photograph) surrounded by a thin layer of secondary wood (white) and a thin cortex (gray). Outside of this is a thick insulating mantle of marcescent leaves. The water-conducting tissues of the stem, as well as the shoot apex, are efficiently protected against the recurrent night frosts. Mount Kenya, Teleki Valley, Kenya, 4,200 m. Photograph by O. Hedberg, 1948, from Hedberg & Hedberg (1979).

FIGURE 4. *Espeletia schulzii* Wedd. Longitudinal section of specimen about 0.8 m tall. Although taxonomically distant from *Senecio keniodendron,* this species has acquired through convergent evolution the same adaptive features providing protection against night frost, e.g., large, nyctinastic leaf rosettes and a mantle of marcescent leaves around the stem. Merida, Mucubaji, Venezuela, 3,600 m. Photograph by I. Hedberg, 1977, from Hedberg & Hedberg (1979).

plausible that at least a third of the angiosperm flora of the world may be of hybrid origin and, hence, very awkward to handle with cladistic methods. This raises some doubt whether evolution has been as parsimonious as cladogram constructors.

Another crucial difficulty for cladistic studies is convergent evolution. One conspicuous example of this is provided by the genera *Dendrosenecio* (East Africa) and *Espeletia* (South America), which both have developed tropical–alpine species with a thick trunk containing a water-storing pith, thick insulating cylinders of marcescent leaves around the stem, and nyctinastic movements of the leaf rosettes (Hedberg & Hedberg, 1979; Figs. 3, 4). Since both genera concerned have less specialized representatives at lower altitudes, there can be no doubt that this is a case of convergent adaptive evolution, and how many less dramatic cases of this occur in the network of evolution we do not know. But we should remember that evolution, like football, is teamwork. It is not brought about only by significant achievements in individuals, single species, or single phyletic lines working in splendid isolation.

Considering that the theories of cladistics are based on a number of outspoken and tacit assumptions and that its methods involve a number of subjective choices, it is difficult to regard it as more empirical or more scientific than either Linnean taxonomy or numerical taxonomy.

My impression is that the Hennigian school has revived the phylogenetic work and speculations pursued by Lotsy (1911) and his contemporaries more than 70 years ago and given it a smart new dress by the adoption of terms like *synapomorphy, symplesiomorphy, autapomor-*

TABLE 1. Subjective estimates of the prospects for and importance of three main types of systematic botanic research from a number of external aspects. The importance is graded in each position from 1 (low) to 3 (high).

Importance aspects for:	Detailed Evolutionary Studies	Floras	Monographs
National political interest	2	3	1
Ease of financing	3	2	1
Meritoriousness	3	1	2
Need for international collaboration	1	3	3
Overall accuracy	2	1	3
Interest to save duplication of effort	2	1	3
Interest for understanding evolution	3	1	3
Necessity for conservation	1	2	3
General scientific value	2	1	3
Urgency	1	2	3

phy, paraphyletic, etc. They have also adopted a formalized handling of character states and taxa which lends itself to graphic presentation and computer treatment. But the facts behind the technology have not seen any important increase. Because of the scarcity of fossil evidence we will probably never be able to check the phylogeny of any substantial parts of the plant kingdom, and in my opinion we should acknowledge that and not pretend that cladistics or any other sort of data manipulation can give us the key to evolution. There is, of course, no harm in summarizing some or all phylogenetic relationships presumed for a group into a cladogram, as long as one acknowledges the limitations behind it. An example of a conservative study of this kind in botany was published by Dahlgren & Rasmussen (1983). But it cannot be avoided that the contrast between the extravagant claims and attire of cladistics as exemplified above and the comparatively meager substance behind it (at least in botany) recalls the famous tale by H. C. Andersen about the emperor and his new clothes.

As we have seen, each new approach or wave of fashion in systematic botany has its limitations. This will certainly also apply to new waves which are bound to come. What I feel is important is that we try to maintain and give to our students a critical approach to such novelties. No new method is likely to provide all the truth and nothing but the truth. And "no scheme of classification can claim more than practical convenience and relatively little violence done to the facts" (Tansley & Chipp, 1926: 6).

Most contributions to systematic botany in the traditional sense may be roughly sorted into three categories: (1) detailed evolutionary studies, (2) revisions for local or regional floras, and (3) monographic work on a global scale. The prospects for and importance of these three approaches have been subjectively estimated in Table 1. The choice between them is obviously by no means free to all botanists.

From a purely scientific point of view, it is of course tempting for most taxonomic botanists to attempt detailed evolutionary studies for small groups, bringing them from α through β towards Ω classification in the sense of Turrill (1950). This requires a substantial amount of time and resources, but the task can be chosen and delimited after the wish of the investigator, who can also decide which methods to employ. It is therefore intellectually stimulating and suitable for Ph.D. studies, which makes it comparatively easy to finance. But the task before us is so enormous, with some 50,000 vascular plant species yet undescribed and vast areas uncollected, that we should pool as much of the available resources as possible to achieve, in the first place, an α or β classification covering all the flora of the world. This may, however, entail a conflict between floras and monographs.

A flora is an indispensable instrument for rational use and conservation of the biological resources and natural environment in any country, and it is understandable that colonial authorities in earlier days put a high priority on the production of floras. Most AETFAT members have certainly been in contact with, and many have contributed to, the work on such manuals as *Flora of Tropical East Africa, Flora Zambesiaca, Flore d'Afrique Centrale, Flore de Madagascar,* etc. But differences of timing and difficulties of financing have often resulted in the same family being treated in separate floras by different botanists with divergent taxonomic views, which implies considerable duplication of effort and possible incompatibility of results.

A better way to utilize the limited botanist resources available evidently would be to get as many botanists as possible started on monographic work on a global scale, from which pertinent data could be extracted for each flora. The desirability of switching the efforts of as many

taxonomic botanists as possible to monographic studies was emphasized by Gillett (1958). A resolution urging UNESCO to support this kind of research was unanimously endorsed by the third general assembly of AETFAT, but no positive response was received fom UNESCO.

Therefore, as expressed by Stace (1980: 245), "Radically new thinking and new arguments are needed if the current fashion for producing floras rather than monographs is to be reversed. Hitherto the purely academic arguments favouring the latter have been outweighed by utilitarian, financial and political arguments . . . . The facts that there are far more widely applicable and useful data contained in monographs, that the preparation of Floras of neighbouring regions often involves much wastefully repetition work on the same taxa, that the writing of Floras would be far more rapid and easy if good monographs were available, and that the need for wide-scale monographing of plant taxa is extremely urgent, need to be brought forcibly to the attention of all those in relevant authority."

There has been much talk and many publications describing what is happening to the tropical rain forest and other species-rich ecosystems. But the recommendations advanced by IUCN, UNEP, WWF, FAO, and UNESCO in the World Conservation Strategy (IUCN, 1980) and, more specifically, by the U.S. National Academy of Science (1980) have had precious little effect as regards increased funding of biological inventories and taxonomic studies of tropical organisms.

Considering the urgency of the Herculean task ahead of us, I suggest that AETFAT members as well as other taxonomic botanists would do best to push on with the taxonomic inventory of Africa and the whole world and publish monographs as quickly as possible. This means that we may have to dispense with some of the modern systematic methods and carry on most of our work at the level of α or β classification so as to get our inventory completed before too many species are gone forever. We should aim at monographing taxa on a global basis whenever possible and attempt to persuade our governments as well as national and international granting bodies to support these activities. Detailed evolutionary studies, however interesting they may be from a purely scientific point of view, should rank lower in interest until we have achieved a workable survey of the world's flora. This will supply an essential documentation infrastructure required to achieve prudent use of our green heritage on a sustained yield basis and conservation of its biological diversity and gene reserves for the benefit of present and future generations.

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TAXONOMIC ANALYSIS OF THE PLANTS DRAWN FROM JAMES BRUCE AND LUIGI BALUGANI'S ETHIOPIAN TRAVELS

F. Nigel Hepper[1]

Abstract

James Bruce was accompanied by Luigi Balugani, an Italian artist who drew the plants and animals encountered during their expedition from North Africa to Ethiopia, from 1765 until Balugani's death in 1771. Analysis of these illustrations and notes, mostly unpublished, provides a record of some 160 species at a time when very little was known about the plants of tropical Africa. Twenty-six new species were based on Bruce and Balugani's material; they noted another 65 unnamed species which were subsequently described from other type material. Balugani is belatedly recognized as a major natural history artist of the eighteenth century.

Résumé

James Bruce était accompagné par Luigi Balugani, un artiste italien qui dessina les plantes et animaux qu'ils rencontrèrent lors de leur expédition de l'Afrique du Nord à l'Ethiopie, de 1765 jusqu'à la mort de Balugani en 1771. L'analyse de ces notes et illustrations, encore non-publiées pour la plupart, fournit un répertoire de quelques 160 espèces à une époque où l'on savait très peu sur les plantes de l'Afrique tropicale. Le matériel de Bruce et Balugani permit de définir 26 nouvelles espèces; ils relevèrent 65 autres espèces non nommées qui furent décrites par la suite à partir de matériel différent. Balugani est tardivement reconnu comme un important peintre naturalist du 18ème siècle.

In a former paper (Hepper, 1980), I outlined the remarkable expedition undertaken by James Bruce of Kinnaird to Ethiopia (Abyssinia) and back in the years 1768–1773. During the tenth plenary meeting of AETFAT in Pretoria, I presented a poster exhibit of reproductions of some of the botanical and zoological drawings made by Luigi Balugani, the artist employed by Bruce, who died before the conclusion of the expedition. The purpose of the present paper is to analyze the botanical discoveries and to assess their scientific value.

At the time of Bruce's journey very little was known about the flora of tropical Africa and nothing about Ethiopian plants; hence, most of those drawn and noted by Balugani were undescribed species. Unfortunately, the opportunity to make them known was lost, as only a few were included in the first edition of *Travels to the Source of the Nile* (Bruce, 1790). In the posthumous second and third editions edited by Alexander Murray (1805, 1813) some more were added, making a total of 34 plates representing 28 species out of some 160 that are now known to have been noted, sketched, or beautifully delineated in watercolor. Most of the published illustrations were named and described by botanists of the day (Appendix I), but all of the others were overlooked and superseded by later collections. While most of the species are Ethiopian, a few were drawn in Syria, Egypt, and Eritrea, and some were drawn from living plants grown at Paris, Florence, Kew, and elsewhere from Bruce's Ethiopian seeds. As far as I can ascertain, 26 species new to science were named from Bruce's material (Appendix I).

However, a great deal of natural history information was accumulated during the expedition and much of it was published in the later editions of *Travels* by Murray, who commented: "The number of beasts, birds, fishes and plants which Mr. Bruce delineated in the course of his travels in Abyssinia, would appear incredible, if he had not brought home his drawings to attest his assiduity in that particular .... As soon as they left Masuah, he and his assistant Balugani began to draw every rare animal, plant and bird which they could discover. They were not scientific botanists nor naturalists, but they proceeded on a first and infallible plan. They painted accurately and beautifully every object which they reckoned curious. They attempted no classification; but all who have seen their drawings have owned that they are such as few painters could

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Monogr. Syst. Bot. Missouri Bot. Gard. 25: 575–580. 1988.

TABLE 1. Summary analysis of plant species recorded by Bruce and Balugani.

Family	Number of Species	Family	Number of Species
	DICOTYLEDONS		
Acanthaceae	3	Moraceae	1
Anacardiaceae	2	Myrsinaceae	1
Annonaceae	1	Oleaceae	3
Apocynaceae	3	Oxalidaceae	1
Asclepiadaceae	7	Phytolaccaceae	1
Avicenniaceae	1	Pittosporaceae	1
Balsaminaceae	1	Proteaceae	1
Boraginaceae	2	Punicaceae	1
Burseraceae	2	Ranunculaceae	2
Campanulaceae	1	Rhamnaceae	2
Capparaceae	2	Rosaceae	1
Celastraceae	2	Rubiaceae	3
Compositae	5	Rutaceae	1
Cucurbitaceae	5	Salicaceae	1
Ebenaceae	2	Santalaceae	1
Euphorbiaceae	5	Sapindaceae	1
Geraniaceae	1	Sapotaceae	1
Hypericaceae	1	Scrophulariaceae	2
Labiatae	9	Simaroubaceae	1
Leguminosae	18	Solanaceae	6
Loganiaceae	2	Sterculiaceae	2
Loranthaceae	2	Tiliaceae	1
Lythraceae	2	Umbelliferae	4
Malvaceae	3	Verbenaceae	1
Melianthaceae	1	Vitidaceae	1
		Total	124
	MONOCOTYLEDONS		
Agavaceae	1	Hydrocharitaceae	1
Amaryllidaceae	3	Iridaceae	1
Cannaceae	1	Liliaceae	10
Commelinaceae	1	Musaceae	2
Cyperaceae	5	Palmae	1
Gramineae	5	Pandanaceae	1
		Total	32
	GYMNOSPERMS		
Cupressaceae	1	Podocarpaceae	1
	ALGAE		1
	UNIDENTIFIED SPECIES		2
		Total	161[a]

[a] Of the 161 plant species, 158 are illustrated.

equal at their leisure, with every opportunity of time and situation.

"The whole collection of natural history which Mr. Bruce drew in Barbary, Arabia and Abyssinia, amounts to about three hundred articles. Of these the plants and birds make the greater part; but all are so highly finished, as to excite the greatest admiration with respect to his taste and abilities."

Murray goes on to comment that Bruce was at a disadvantage as a traveler, being unable to stop and watch the growth and phenology of "a tree from which he pulled a branch as he passed along." However, "he always committed to paper a short description of whatever was drawn by him and his assistant and in general on the paper which contained the sketch" (Murray, 1805, 1813). This observation is perfectly true, for al-

most every sheet has copious notes surrounding the sketch, and it is worthwhile crediting Luigi Balugani with both the drawings and the notes—something that Murray seemed reluctant to do in spite of the fact they are written in Italian in Balugani's hand. As leader of the expedition, Bruce gains reputation for all that is accomplished on it, so in this sense the results may be attributed to Bruce.

Murray muses that if the entire collection had been published by Bruce or "by some eminent naturalist, who could have arranged the different articles according to the Linnean system and made observations on their genera and species, . . . it would have furnished a splendid proof of his industry and care as well as a considerable addition to natural knowledge." At last this has come to fruition as far as the plants are concerned, with their forthcoming publication in a volume prepared by P. Hulton, F. N. Hepper, and I. Friis (in press), to be published by A. A. Balkema in association with the Yale Center for British Art. The arrangement is not by the "Linnean system" as recommended by Murray, but alphabetically according to family, genus, and species, with relevant synonymy and notes. A summary analysis is given in Table 1.

All of the drawings are being reproduced in our volume and, for the first time, many of them are printed in color. As mentioned above, the black-and-white sketches are surrounded by copious field notes written by Balugani in Italian. The notes include a vernacular name for more than 100 species, usually in Amharic or Tigrinia, which Murray considered "would afford little information to the reader, especially as these names cannot be translated without considerable danger of mistake." Nowadays it is possible to check their accuracy against those published by Schweinfurth (1893, 1896), Cufodontis (1953–1972), Mooney (1963), and others, and it is gratifying to record that almost without exception they have proved to be reliable.

When one realizes that Luigi Balugani was not a trained botanist (although one suspects he must have had some background in natural history, as he used scientific terminology), it is remarkable how observant he was. In one of his sketches he notes the arrangement of leaves on a stem of *Protea gaguedi,* working out the fractions, and he was probably the first to recognize phyllotaxis.

Species Described after 1790

If one takes 1790, the year of publication of *Travels,* as the baseline, it is interesting to assess the number of species that would have been new to science had they been described and named in 1790.

Table 2. Species described after 1790 (description of species of basionym).

Group 1: 1790–1849

Clausena anisata (1799), *Jasminum dichotomum* (1804), *Pittosporum viridiflorum* (1814), *Boswellia papyrifera* (1826), *Vernonia amygdalina* (1826), *Ehretia cymosa* (1827), *Gardenia ternifolia* (1827), *Hygrophila auriculata* (1827), *Clematis hirsuta* (1830), *Bersama abyssinica* (1837), *Saba comorensis* (1837), *Pynostachys abyssinica* (1838), *Trifolium polystachyum* (1839), *T. rueppellianum* (1839), *Echinops macrochaetus* (1840), *Clerodendron myricoides* (1842), *Dregea abyssinica* (1843), *Nuxia oppositifolia* (1843), *Ruttya speciosa* (1843), *Acokanthera schimperi* (1844), *Diospyros mespiliformis* (1844), *Discopodium penninervium* (1844), *Jasminum abyssinicum* (1844), *Kniphofia foliosa* (1844), *Astragalus atropilosulus* (1846), *Millettia ferruginea* (1846), *Verbascum sinaiticum* (1846), *Alepidea peduncularis* (1847), *Diplolophium africanum* (1847), *Grewia ferruginea* (1847), *Hypericum quartinianum* (1847), *Juniperus procera* (1847), *Loranthus globiferus* (1847), *Rhus glutinosa* (1847), *Woodfordia uniflora* (1847), *Ziziphus abyssinica* (1847), *Abutilon longicuspe* (1849), *Ottelia ulvifolia* (1849).

Group 2: 1850–1899

Albizia malacophylla (1851), *Croton macrostachyus* (1851), *Oenostachys abyssinica* (1851), *Solanum adoense* (1851), *S. piperiferum* (1851), *Tacazzea galactogoga* (1854), *Osyris lanceolata* (1857), *Isodon ramosissimus* (1862), *Impatiens rothii* (1868), *Rhus ? retinorrhoea* (1868), *Coleus edulis* (1871), *? Peponium vogelii* (1871), *Diospyros abyssinica* (1873), *Aloe macrocarpa* (1875), *Senecio gigas* (1875), *Crinum schimperi* (1889), *Maytenus argutus* (1893), *Arundinaria alpina* (1895), *Dracaena steudneri* (1895), *Pycnostachys eminii* (1895), *Trifolium usambarense* (1895).

Group 3: 1900 onwards

Podocarpus gracilior (1903), *Ritchiea albersii* (1903), *Delphinium wellbyi* (1907), *Euphorbia nubica* (1911), *Sansevieria abyssinica* (1913), *Acanthus sennii* (1940).

In Table 2, the new plants are arranged in groups according to when they were first described (i.e., the basionym, whether in the same genus or another one to which they have since been transferred). There are three arbitrary groups in order to show more clearly how long after Bruce's expedition the same species were described by other botanists—38 species were described between 1790 and 1849, 21 species from 1850 and 1899, and six species after 1900.

The first group covers the period of great botanical explorations in Ethiopia by such as W.

G. Schimper, A. Petit and Quartin-Dillon; so it is the largest, with most species being described in the 1830s and 1840s, some 50–60 years after Bruce's expedition. The second group, with 21 species, covers the centenary period after Bruce's expedition during which the early volumes of the *Flora of Tropical Africa* were published, and it is a pity that many of Bruce's species were not known earlier so that they could have been included in this work. Perhaps the third group is the most surprising in that any of Bruce's species remained until the twentieth century to be named and described—one of the five species actually waited until 1940, and a conspicuous scarlet-flowered one too.

There is no doubt that had Bruce been able to afford to publish all of his illustrations, the botany (and zoology) of tropical Africa would have been known much sooner and Bruce himself would have gained more credit for natural science than he generally receives. In fact, we are concluding that much of the credit should now be given to his assistant Luigi Balugani, who emerges from obscurity to full stature as a major botanical and zoological artist.

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Appendix 1.

New species of plants based on Bruce's material. (For more complete notes, see Hulton et al., in press.)

Dicotyledons

Avicenniaceae

Avicennia marina (Forssk.) Vierh., Denkschr. Akad. Wien, Math.-Nat. 71: 435. 1907.

"Rack" Bruce, Travels, ed. 1, 5: 44–46, pl. opposite p. 44 (1790); ed. 2, 7: 157–158 & 8: pl. 12 (1805); ed. 3, 7: 173–174 & 8: pl. 12 (1813).

Racka torrida J. F. Gmel., Syst. Nat., ed. 13, 2: 245. 1791. Type: Eritrea. Bruce's plate. The new genus *Racka* J. F. Gmel., Anh. J. Bruce Reisen: 64 (1791) & Syst. Nat., ed. 13, 2: 213 (1791) was based on Bruce's plate and description.

Boraginaceae

Cordia africana Lam., Tabl. Encyc. Ill. 1: 420 No. 1896. 1792.

"Wanzey" Bruce, Travels, ed. 1, 5: 54–56, pl. opposite p. 54 (1790); ed. 2, 7: 164–166 & 8: pl. 17 (1805); ed. 3, 7: 180–182 & 8: pl. 17 (1813).

Cordia abyssinica R. Br. in Salt, Voy. Abyss., App.: lxiv. 1814. Type: Ethiopia. Bruce's plate.

Compositae

Guizotia abyssinica (Linn. f.) Cass., Dict. Sci. Nat. 59: 237, 248. 1829. Type: Ethiopia: Bruce's specimen or plate as below.

"Nuk" Bruce, Travels ed. 2, 7: 337–339 & 8: pl. 52 (1805); ed. 3, 7: 353 & 8: pl. 52 (1813).

Polymnia abyssinica Linn. f., Suppl. Plant. 383. 1781. Originated in Ethiopia, but grown at Paris. No herbarium specimen found at P, but one in LINN might be a type.

Polymnia frondosa Bruce ex Murray, Travels, ed. 2, 7: 337–339 & 8: pl. 52 (1805); ed. 3, 7: 353 & 8: pl. 8 (1813). Type: Ethiopia. Bruce's plate.

Cucurbitaceae

Coccinia abyssinica (Lam.) Cogn. in DC., Monogr. Phan. 3: 536. 1881.

Bryonia abyssinica Lam., Encyc. 1: 497. 1784. Type: Cultivated in France from seeds brought from Ethiopia by Bruce, type specimen in P-LA.

Euphorbiaceae

Euphorbia abyssinica J. F. Gmel., Syst. Nat., ed. 13, 2: 759. 1791. Type: Bruce's plate as below and drawings at Yale.

"Kol-qual" Bruce, Travels, ed. 1, 5: 41–44 & two plates opposite p. 41 & 43 (1790); ed. 2, 7: 154–156 & 8: pls. 10, 11 (1805); ed. 3, 7: 170–172 & 8: pls. 10, 11 (1813).

Euphorbia officinarum var. *kolquall* Willd., Sp. Pl. 2: 884. 1799. Type: Ethiopia. Bruce's plates.

Labiatae

Salvia nilotica Juss. ex Jacq., Hort. Vindob. 3: 48, t. 92. 1776. Types: five isotypes at W, presumably grown there or at Paris from Bruce's Ethiopian seeds.

Salvia abyssinica Linn. f., Suppl. Plant. 88 (1781); Jacquin, Ic. Pl. rar. 2, t. 6 (1781) & Collect. 1: 132 (1787). Type: Jacquin's plate, which was probably drawn from the type specimens of *S. nilotica*.

Leguminosae

Albizia gummifera (J. F. Gmel.) C. A. Smith, Bull. Misc. Inf. Kew 1930: 218. 1930.

"Sassa" Bruce, Travels, ed. 1, 5: 27, two pl. opposite p. 27 (1790); ed. 2, 7: 141–147 & 8: pl. 4 & 5 (1805); ed. 3, 7: 157–163 & 8: pl. 4 & 5 (1813).

Sassa gummifera J. F. Gmel., Syst. Nat., ed. 13, 2: 1038. 1791. Type: Ethiopia. Bruce's plate.

Mimosa sassa Bruce, Travels (ed. Castera): 6, pl. 4 & 5. 1792.

Bauhinia farec Desv., J. de Bot. 3: 74. 1814. Type: Ethiopia. Bruce's plate.

"Farek" or *Bauhinia acuminata* Bruce, Travels, ed. 1, 5: 57, pl. opposite p. 57 (1790); ed. 2, 7: 167–174 & 8: pl. 18 (1805); ed. 3, 7: 183–190 & 8: pl. 18 (1813), non L. Type: Ethiopia. Bruce's plate.

One of the most notable discoveries, since it has never been re-collected, yet evidently a perfectly distinct species. In 1982, Mats Thulin attempted to find it in its original locality at Geesh, but he fears it is extinct owing to degradation of the vegetation.

Crotalaria pallida Aiton, Hort. Kew. 3: 20. 1789. Type: specimen at BM prepared from a plant cultivated at Kew from seeds collected by Bruce in Ethiopia.

Dichrostachys cinerea (L.) Wight & Arn., Prodr. Fl. Pen. Ind. Or.: 271. 1834.

"Ergett y 'dimmo' " Bruce, Travels, ed. 1, 5: 34, pl. opposite p. 34 (1790); ed. 2, 7: 147–148 & 8: pl. 6 (1805); ed. 3, 7: 163–164 & 8: pl. 6 (1813).

Mimosa sanguinea J. F. Gmel., Syst. Nat., ed. 13, 2: 803. 1791. Type: Ethiopia. Bruce's plate.

Erythrina abyssinica DC., Prodr. 2: 413. 1825. Type specimen at Geneva (G) raised in Paris from seeds brought from Ethiopia by Bruce. The plate of "Kuara" included fruits of *E. abyssinica* on branches of *E. brucei*.

Erythrina brucei Schweinf. emend Gillett in Kew Bull. 15: 428, pl. 3 & fig. 1. 1962. Type: Bruce's plate (excluding fruits and seeds, which are of *E. abyssinica*).

"Kuara" Bruce, Travels, ed. 1, 5: 65–66 & pl. opposite p. 65 (1790); ed. 2, 7: 174–175 & 8: pl. 19 (1805); ed. 3, 7: 190–191 & 8: pl. 19 (1813).

Mimosa pigra L., Cent. I. pl. 1: 13. 1755.

"Ergett el Krone" Bruce, Travels, ed. 1, 5: 35–36, pl. opposite p. 35 (1790); ed. 2, 7: 148–149 & 8: pl. 7 (1805); ed. 3, 7: 164–165 & 8: pl. 7 (1813).

Mimosa cornuta J. F. Gmel., Syst. Nat., ed. 13, 2: 804. 1791. Type: Ethiopia. Bruce's plate.

Pterolobium stellatum (Forssk.) Brenan, Mem. N.Y. Bot. Gard. 8: 425. 1954.

"Kantuffa" Bruce, Travels, ed. 1, 5: 49–51, pl. opposite p. 49 (1790); ed. 2, 7: 160–163 & 8: pl. 14 (1805); ed. 3, 7: 176–179 & 8: pl. 14 (1813).

Cantuffa exosa J. F. Gmel., Syst. Nat., ed. 13, 2: 677. 1791. Type: Ethiopia. Bruce's plate.

Acacia kantuffa Poir., Encycl. Suppl. 5: 529. 1817. Type: Ethiopia. Bruce's plate.

Loganiaceae

Buddleia polystachya Fresen. in Flora 21: 605. 1838.

"Umfar" or "Amfar" Bruce, Travels, ed. 2, 7: 339–340 & 8: pl. 53 as "Umfar" or "Lentana" (1805); ed. 3, 7: 355–356 & 8: pl. 53 (1813).

B. acuminata R. Br. in Salt, Voy. Abyss., App.: lxiii. 1814. Non Poir. 1811. Type: Ethiopia. Bruce's plate.

Phytolaccaceae

Phytolacca dodecandra L'Hérit., Stirp. Nov. t. 69. 1791. Type: Plants were grown in Paris from seeds brought back from Ethiopia by Bruce, but no herbarium specimens have been found. In lieu of a specimen, the figure should be considered the type.

Proteaceae

Protea gaguedi J. F. Gmel., Syst. Nat., ed. 13, 2: 225. 1791. Type: Ethiopia. Bruce's plates as below.

"Gaguedi" Bruce, Travels, ed. 1, 5: 52–53, two pl. opposite p. 52, 53 (1790); ed. 2, 7: 163–164 & 8: pl. 15 & 16 (1805); ed. 3, 7: 179–180 & 8: pl. 15 & 16 (1813).

Rosaceae

Hagenia abyssinica (Bruce) J. F. Gmel., Syst. Nat. 13, 2: 613. 1791. Type: Ethiopia. Bruce's plates as below. The genus *Hagenia* J. F. Gmel. was founded on Bruce's description and plates.

"Cusso" or *Banksia abyssinica* Bruce, Travels, ed. 1, 5: 73–75 & two plates as *Bankesia* (1790); ed. 2, 7: 181–184 & 8: pl. 22 & 23 (1805); ed. 3, 7: 197–200 & 8: pl. 22 & 23 (1813). Type: Ethiopia. Bruce's plates.

Sapotaceae

Mimusops kummel Fresen, Flora 21: 605. 1838. A.DC., Prodr. 8: 203. 1844. Type: Ethiopia. Bruce's plates as below.

"Kummel" Bruce, Travels, ed. 2, 7: 341–342 & 8: pl. 54 (1905); ed. 3, 7: 357–358 & 8: pl. 54 (1813).

Simaroubaceae

Brucea antidysenterica J. Miller, Icones: 25. 1779. Type: specimen at BM of a plant raised at Kew from seed brought back from Ethiopia by Bruce.

Solanaceae

Solanum marginatum Linn. f., Suppl. Pl.: 147. 1781. Type: the description was based on a plant that must have been grown in France from seeds brought from Ethiopia by Bruce, but no herbarium specimen has been found; the plate should be taken as the type.

Sterculiaceae

Dombeya torrida (J. F. Gmel.) Bamps, Bull. Jard. Bot. Brux. 32: 170. 1962.

"Walkuffa" Bruce, Travels, ed. 1, 5: 67–68 & pl. opposite p. 67 (1790); ed. 2, 7: 176–177 & 8: pl. 20 (1805); ed. 3, 7: 192–193 & 8: pl. 20 (1813).

Walcuffa torrida J. F. Gmel., Syst. Nat. 13, 2: 1029. 1791. Type: Ethiopia. Bruce's plate.

Dombeya bruceana A. Rich., Tent. fl. abyss. 1: 77. 1847. Syntypes: Bruce's plates; *Schimper 1370*; & *Quarton-Dillon s.n.* The genus *Walcuffa* J. F. Gmel. (*Walkuffa* Bruce ex Steud.) was created to accommodate this species.

MONOCOTYLEDONS

Gramineae

Eragrostis tef (Zucc.) Trotter, Soc. Bot. Ital. 1918: 62, in obs. 1918.

"Teff" Bruce, Travels, ed. 1, 5: 76–80 excl. pl. opposite p. 76 (1790). Note that the plate does not belong to the description and was a longstanding source of confusion.

Poa tef Zucc., Diss. Tef: 21. 1775. Type: plants grown in the Botanical Garden of Florence from seeds collected by Bruce in Ethiopia, but no herbarium specimen found in Florence (but see below).

Poa abyssinica Jacq., Misc. 2: 364. 1781. Type: herbarium specimen and watercolor at W evidently grown at Vienna.

Ischaemum afrum (J. F. Gmel.) Dandy in F. W. Andrews, Fl. Pl. Sudan 3: 476. 1956.

"Gir gir" or "Gesheel aube" Bruce, Travels, ed. 1, 5: 47–48, pl. opposite p. 47 (1790); ed. 2, 7: 159–160 & 8: pl. 13 (1805); ed. 3, 7: 175–176 & 8: pl. 13 (1813).

Andropogon afer J. F. Gmel., Syst. Nat., ed. 13, 2: 166. 1791. Type: Ethiopia. Bruce's plate.

Liliaceae

Albuca abyssinica Murray, Syst. Veg.: 326. 1784. Jacquin, Collect. 1: 55. 1787. Type: although described from a living plant at Paris presumably grown from seeds or bulbs brought from Ethiopia by Bruce, no herbarium specimen has been found; Jacquin's plate should be considered to be the type in lieu of a specimen.

Musaceae

Ensete ventricosum (Welw.) Cheesman, Kew Bull. 2: 101. 1947.

"Ensete" Bruce, Travels, ed. 1, 5: 36, pl. opposite p. 36 & 37 (1790); ed. 2, 7: 149–153 & 8: pl. 8 & 9 (1805); ed. 3, 7: 165–166 & 8: pl. 8 & 9 (1813). The new genus *Ensete* Bruce was Bruce's important discovery.

Musa ensete J. F. Gmel., Syst. Nat., ed. 13, 2: 567. 1791. Type. Ethiopia. Bruce's plates.

TAXONOMIC PROBLEMS IN THE GENUS *DOROTHEANTHUS* (MESEMBRYANTHEMACEAE)

HANS-DIETER IHLENFELDT[1]

ABSTRACT

Subtribe Dorotheanthinae comprises three genera of short-lived annual plants with slightly succulent leaves. In some respects Dorotheanthinae reflect the general taxonomic situation in Mesembryanthemaceae: besides a number of distinctive and homogeneous taxa of restricted distribution, there are large heterogeneous complexes with a wide distribution and a wide range of variation in relevant taxonomic characters connected by transitions, so that it is difficult to define taxa. This is especially true for the *Dorotheanthus bellidiformis* complex (15 described species), ephemeral plants adapted in the past to rare habitats—open places with wind-shifted sand. The seeds have an abnormal thin seed coat and probably can only survive buried in the ground once they are released from the capsules. The capsule types can be arranged in a morphological sequence which may be interpreted as an ecocline running from south to north parallel to decreasing annual rainfall. Field studies revealed that there is no correlation between capsule morphology and other characters (including the flower) and that there are numerous intermediate populations. While in the past taxa of this complex have been stabilized by extreme isolation (in space and time), in recent time they obviously started ample gene exchange. This has been caused by the enormous increase of suitable habitats due to the progressing devastation of the natural vegetation cover by expanding agriculture. In the future this complex will probably form one single gene pool with no discontinuities at all.

RÉSUMÉ

D'une certaine façon, la sous-tribu Dorotheanthinae, un groupe de plantes annuelles ephémères avec des feuilles légèrement succulentes, reflète la situation taxonomique générale dans les Mesembryanthemacées: outre un nombre de taxons bien définis et homogènes de répartition restreinte, il y a des complexes hétérogènes importants avec une répartition large et une grande variation de caractéristiques taxonomiques significatives qui sont reliés par des formes de transition, ce qui rend les taxons difficile à définir. Ceci est particulièrement vrai dans le cas du complexe de *Dorotheanthus bellidiformis* (15 taxons décrits), des plantes qui occupaient sans doute autrefois des habitats rares: dans des espaces ouverts avec du sable soulevé par le vent. Les graines ont un integument anormalement mince et ne peuvent probablement survivre qu'enfouies dans le sol une fois qu'elles émergent des capsules. Les types de capsules de ce complexe peuvent être rangés en ordre morphologique qui peut être interprété comme un ecocline orienté sud-nord qui est parallèle à une ligne de pluviosité annuelle décroissante. Dans la plupart des cas il n'y a pas de rapport entre la morphologie des capsules et les autres caractères (y compris la fleur), et il y a de nombreuses populations intermédiaires. Il se peut qu'autrefois les taxons aient été stabilisés par une isolation extrême (dans l'espace aussi bien que dans le temps), mais récemment elles ont commencé un échange génétique important. Ceci est causé par une augmentation énorme d'habitats propices dûs à la dévastation progressive de la végétation naturelle par l'agriculture. Dans un avenir proche, ce complexe formera probablement un seul reservoir génétique sans discontinuités.

The subtribe Dorotheanthinae comprises three genera of short-lived annual plants with only slightly succulent leaves: *Dorotheanthus* Schwantes, *Cleretum* N. E. Br., and *Aethephyllum* N. E. Br. *Dorotheanthus bellidiformis* (Burm.) N. E. Br., the Livingstone Daisy, is widely cultivated as an ornamental annual for its decorative flowers marvellously colored by betalains, and *Aethephyllum pinnatifidum* (L. f.) N. E. Br. is often found in botanical gardens. There has been a long debate on the correct names of these genera, but this problem is now settled (Struck & Ihlenfeldt, 1985).

Although the fruit characters, which are generally extremely important for the delimitation of taxa within Mesembryanthemaceae, exhibit an extraordinary range of variation in Dorotheanthinae (which in other parts of the family would separate even subtribes), the reticulate distribution of nearly all other characters indicates that all taxa are closely related, i.e., form a natural group. Although taxa of this subtribe do not have one single character that is shared by all members and at the same time is restricted to this group, it appears to be well separated from all other groups of subfamily Ruschioideae. This

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FIGURE 1. Seed of *Dorotheanthus maughanii* (subg. *Pherelobus*). The thick testa is sculptured and contains tannins. Scale bar = 1 mm.

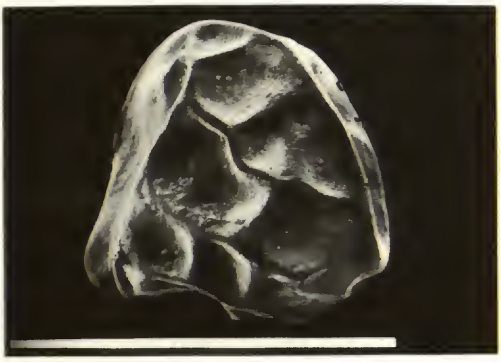

FIGURE 2. Seed of *Dorotheanthus bellidiformis* (subg. *Dorotheanthus*). The thin testa is smooth and translucent. The shape of the seed is flat. Scale bar = 1 mm.

suggests an early segregation of this group and a long independent evolution.

In some respects Dorotheanthinae reflect the general taxonomic situation in Mesembryanthemaceae. Besides a number of distinctive and homogeneous taxa with a restricted distribution, there are large heterogeneous complexes with a wide distribution and a wide range of variation in relevant taxonomic characters connected by transitions, so that it is extremely difficult to delimit taxa. Within Dorotheanthinae this is especially true for *Dorotheanthus*. In this paper, the phylogeny and the taxonomic problems of this genus will be discussed in some detail.

Based on leaf form, capsule morphology, and seed structure, *Dorotheanthus* can be divided into two subgenera: 1) Subgenus *Pherelobus* (N. E. Br.) Ihlenf. & Struck, with only two distinct taxa of specific rank and very restricted distribution: *Dorotheanthus maughanii* (N. E. Br.) Ihlenf. & Struck and *D. boysenii* L. Bolus. The leaves are distinctly spathulate and covered by extremely large bladder cells, and the seeds are dark and have a distinct sculpturing (Fig. 1). 2) Subgenus *Dorotheanthus*. The leaves are indistinctly spathulate to linear, the bladder cells are much less prominent; the taxa are notably characterized by the flat, triangular seeds with no sculpturing of the testa (Fig. 2), which are unique within the subtribe. The white color of the seeds is caused by an extremely thin, translucent seed coat containing almost no tannins.

There are indications that because of the extremely thin seed coat, seeds of the latter subgenus can only survive if they are buried in the ground once they are released from the capsules. This special feature obviously restricts the occurrence of these taxa to habitats in which the soil is sandy and is turned over by some agent, normally the wind. The smooth testa and the flat seed shape apparently help the seeds to become buried in the soil. It can be supposed that in the past, taxa of subgenus *Dorotheanthus* occurred only in a few isolated (in space as well as in time) populations due to the scarcity of suitable ecological niches. Under natural conditions within the distribution area of this subgenus, shifting sand can only be expected on dunes, in river beds, and after the destruction of the vegetation of woody plants by bush fires. This assumption is supported by the notable fact that, in spite of the showy flowers, there are few gatherings from natural habitats before 1900; nearly all herbarium collections made before 1900 represent material from cultivation.

PHYLOGENY OF SUBGENUS *DOROTHEANTHUS*

All taxa of Dorotheanthinae possess the hygrochastic capsule typical of Mesembryanthemaceae (Ihlenfeldt, 1983). In subgenus *Dorotheanthus* seven capsule types can be distinguished, ranging from those with only rudimentary cell lids to capsules with complete lids (Figs. 3–5). In the first type, the seeds in the locules lie exposed when the opening mechanism of the capsule (which consists of dead cells capable of swelling when wetted) has turned back the five valves (Fig. 5); in the latter type, the seeds are still covered by two membranes that leave only a tiny opening at the outer margin of the capsule for the seeds to escape (Fig. 4). Only capsule types 6 and 7 (Fig. 3) have distribution ranges that may be considered as well separated (Fig. 6); those of the types 3, 4, and 5 form a sort of mosaic; and the ranges of types 1 and 2 over-

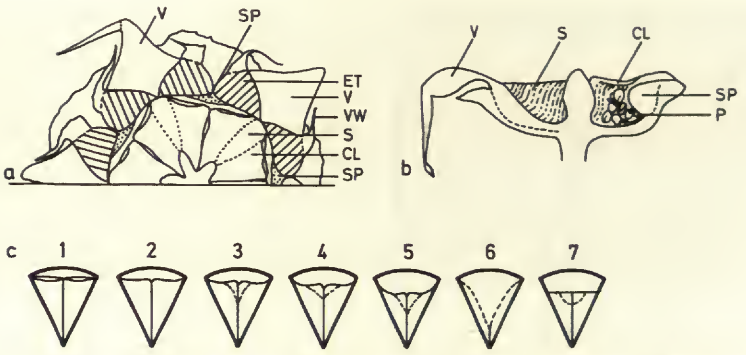

FIGURE 3. Capsule types of the subgenus *Dorotheanthus*.—a. Open capsule (type 1) seen from above; the five locules are covered by nearly complete cell lids.—b. Longitudinal section.—c. Sketches of a single locule of each of the seven types, demonstrating the different degree of cell lid formation; the dotted lines indicate variability. The capsule types differ in additional features not shown in these drawings. ET = expanding tissue, V = valve, VW = valve wing (originating from the splitting of an incomplete false septum), S = septum, CL = cell lid, SP = sealing protuberance that narrows the opening of the locules, L = locule, P = placenta.

lap. Nevertheless, it is obvious that the capsule types comprise a topocline running from south to north. Types 1 to 6 form a morphological sequence from complete cell lids to nearly none (taxa with the latter type have been placed in a separate genus, *Sineoperculum* Jaarsveld); type 7 resembles type 5 in respect to the degree of cell lid formation.

It is generally accepted that within Mesembryanthemaceae the evolution of the capsule types runs from types without cell lids to types with complicated auxiliary structures such as cell lids, which improve the basic dispersal system by raising the maximum distance seeds can be ejected by raindrops, and by lengthening the duration of release (Ihlenfeldt, 1983). Therefore, one is inclined to read the sequence of capsule types from 6 (lacking cell lids) to 1 (complete cell lids). In this special case this is obviously wrong, because the topocline mentioned above is an ecocline following decreasing annual rainfall from south to north (average annual rainfall is 425 mm in the south, 150 mm in the distribution range of type 6). While taxa with capsule type 1, due to sufficient rainfall, have a good chance to develop every year, taxa with type 6 capsule probably reproduce (which is essential for a true annual) only in years with rainfall far above average. Generally, in *Dorotheanthus* the capsules are rather fragile; under natural conditions those of type 1 may last as long as the beginning of the next rainy season when seeds are released and dispersed by rain, but those of type 6 start to disintegrate after five months and before the be-

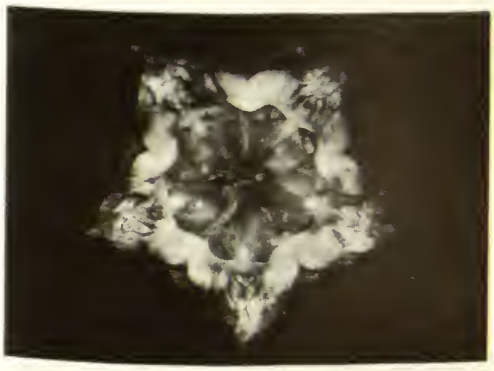

FIGURE 4. Open capsule of *Dorotheanthus bellidiformis* subsp. *bellidiformis* seen from above (capsule type 1, Fig. 3). The locules are almost completely covered by cell lids. ×4.

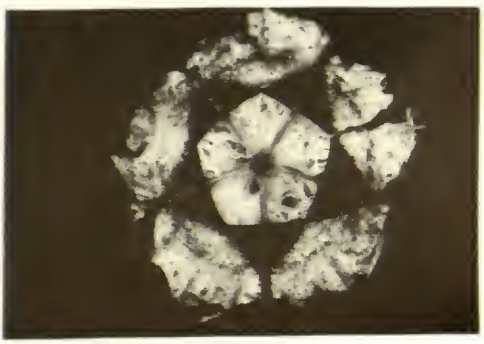

FIGURE 5. Open capsule of *Dorotheanthus rourkei* seen from above (capsule type 6, Fig. 3). Cell lids are reduced to narrow fringes. ×4.

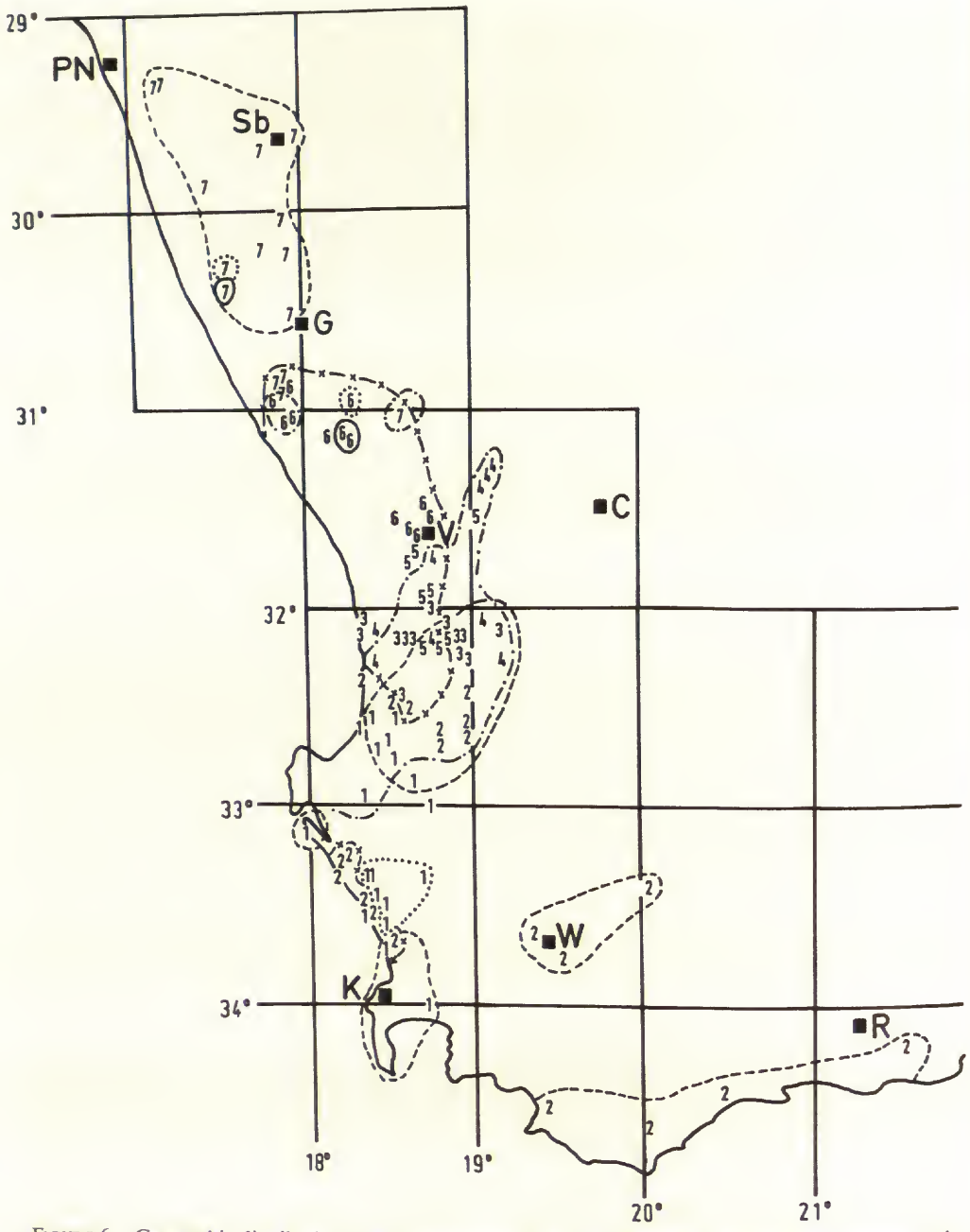

FIGURE 6. Geographic distribution of the capsule types (Fig. 3) in subgenus *Dorotheanthus* (representative populations) and the distribution of flower colors. ····· white, –·–·– yellow, – – – red violet, — × — orange, —— red.

ginning of the next rainy season. Under the ecological conditions in the northern part of the range, plants may not grow for many years. Complicated capsules therefore do not confer any selective advantage. In order to cope with the high loss of seedlings, under these conditions it is a much better strategy to concentrate on seed production rather than on formation of complicated

capsules that require high investments of organic matter, provided the seeds are capable of surviving outside the capsule (see above). Thus the relation between organic matter invested in seeds and organic matter invested in capsules has been shifted in the direction of seeds in capsule type 6. Therefore, in subgenus *Dorotheanthus* the range of capsule types should be read as a sequence of regressive evolution from type 1 to type 6, induced and stabilized by ecological factors. This interpretation is supported by the condition in subgenus *Pherelobus,* which, judging from seed structure and certain features of the opening mechanism of the capsule, is more primitive but has complete cell lids. It is very probable that after having developed special adaptations for colonizing ephemerical ecological niches (see above), the radiation of *Dorotheanthus* took place from south to north, from wetter (favorable) to dryer (less favorable) areas.

The Taxonomic Situation in Subgenus *Dorotheanthus*

Within subgenus *Dorotheanthus,* two species, both with capsule type 2, *D. gramineus* (Haw.) Schwantes and *D. apetalus* (L. f.) N. E. Br., are distinguished morphologically from the other species by their linear leaves and special ecological niches. They are halophytes. *Dorotheanthus apetalus* prefers sites in range of ocean spray and is furthermore characterized by the reduction of the petals (petaloid staminodes), so the flowers are not showy. This tiny species is widespread but often overlooked due to its inconspicuous flowers. *Dorotheanthus apetalus* and *D. gramineus* may occur sympatrically, but no natural hybrids have been observed between them nor with other taxa of the subgenus, so that they appear well separated and deserve specific rank.

The rest of the subgenus forms a complex of 15 described species, based mainly on flower characters, such as color and form of the petals, and certain features of the stamens. An analysis based on a broad sampling from many populations revealed that these characters, except color, are distributed at random throughout the populations. This may be interpreted as evidence that they have no selective value and are the result of genetic drift in small isolated populations, a phenomenon well known from other genera of the family, e.g., *Monilaria* (Schwantes) Schwantes (Ihlenfeldt & Jörgensen, 1973).

If one compares the distribution of the flower colors with the distribution of the capsule types (Fig. 6), one recognizes large areas of different colors that do not coincide with the areas of the capsule types. Where populations of taxa defined by capsule types 3 to 5 are in direct contact, it has frequently been observed that they exhibit different flower colors. In these cases numerous hybrids have been observed and can be recognized easily by their intermediate color. From these observations, one can conclude that taxa defined by the capsule types 1 to 5 have no genetic barriers that prevent gene exchange; this is in accordance with observations in cultivated material. As has been pointed out earlier, it is probable that in the past populations of these taxa were well isolated by the lack of suitable habitats. But today, being winners in the progressive devastation of the natural vegetation cover by expanding agriculture, the isolation has broken down, and all taxa exhibiting capsule types 1 to 5 now form one single gene pool. It can be expected that in the near future the populations will form a continuum as far as characters of no selective value are concerned. Of all characters mentioned, there seem to be only two exceptions: the capsule types, which probably will be further stabilized by ecological conditions, and flower color. As is known from other examples in the family, there is a strong selective pressure towards uniformity of flower color within populations. This may explain the above-mentioned observation that large distribution areas with uniform flower color do not coincide with areas of capsule types. It may be that in the end all populations, as far as they have regular gene exchange, will have the same uniform flower color. There are, however, some indications that due to the intervention of the main competitors for the pollinators (Müllerian mimicry), several different flower colors may become stabilized, i.e., represent a system of stabilized polymorphism.

One can interpret the present distribution of capsule types and flower colors as progressive equalization by ample gene exchange caused by the extension of agricultural activities of man. Starting in the south where it is already well advanced, it has now reached the middle of the range, while the north (capsule types 6 and 7) has up to now been little affected. This may also be due to the fact that in these parts the plants do not develop regularly every year, which may hamper rapid gene exchange. So far, no natural

hybrids between taxa with capsule types 6 and 7 and neighboring taxa have been observed.

From this discussion, it is clear that it is impossible at present to delimit any taxa in the complex of populations that exhibit capsule types 1 to 5. We believe it adequate to treat this whole complex as one species (*Dorotheanthus bellidiformis*). The plant with the capsule type 6 (*D. rourkei* L. Bolus) may still deserve specific rank, since up to now there are no indications of frequent gene exchange with neighboring taxa. The taxon with the capsule type 7, which also still seems to be fairly well isolated but which is morphologically very similar to *D. bellidiformis,* may deserve subspecific rank (subsp. *hestermalensis* Ihlenf. & Struck).

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PROGRÈS ACCOMPLIS DANS LA CONNAISSANCE DE LA FLORE PHANÉROGAMIQUE AFRICAINE DE 1953 À 1979

J. LEJOLY[1] ET M. GABRIEL[2]

RÉSUMÉ

Les statistiques sur le nombre de nouveaux genres, espèces, combinaisons, et taxons intraspécifiques ont été réalisées en consultant les AETFAT Index publiés par le Laboratoire de Botanique systématique et de Phytosociologie de l'Université libre de Bruxelles. Une attention particulière a été accordée sur la période 1977 à 1979 pour laquelle les AETFAT Index viennent d'être constitués. La flore africaine est encore loin d'être bien connue puisqu'au cours des années 1977 à 1979, 596 espèces nouvelles ont encore été décrites, soit 199 en moyenne par année. Néanmoins, cette moyenne est nettement plus faible que celle correspondant à la période 1953–1963; à cette époque, 422 espèces nouvelles étaient décrites en moyenne chaque année. Par contre, le nombre de combinaisons nouvelles se maintient à un niveau élevé et on constate même qu'au cours des dernières années, le nombre de combinaisons nouvelles devient nettement supérieur au nombre d'espèces nouvelles; la tendance à modifier le statut des taxons l'emporte par rapport aux descriptions de nouveaux taxons.

ABSTRACT

Data have been gathered on the number of new genera, species, combinations, and infraspecific taxa by consulting the AETFAT Indices published by the Laboratoire de Botanique Systématique et de Phytosociologie at the Université Libre de Bruxelles. Particular attention has been paid to the period from 1977–1979 for which the AETFAT Indices have recently been completed. The African flora is still far from being well understood, since, during the years 1977–1979, 596 new species were described, an average of 199 per year. Nevertheless, this average is considerably less than that for the period 1953–1963, during which time an average of 422 new species were described per year. By contrast, the number of new combinations remains at a high level, and we have noted that during the last few years the number of new combinations has become clearly greater than the number of new species. The tendency to modify the status of taxa has surpassed the description of new taxa.

Les statistiques des progrès accomplis dans la connaissance de la flore phanérogamique africaine de 1953 à 1979 ont été réalisées en consultant les AETFAT Index publiés par le Laboratoire de Botanique systématique et de Phytosociologie de l'Université libre de Bruxelles (Léonard, 1954–1977; Lejoly et al., 1985a, b).

Dans ces calculs, nous faisons intervenir les données correspondant aux années 1977 à 1979 pour lesquelles les AETFAT Index viennent d'être constitués. Nous disposons ainsi d'une série de données s'étendant sur 27 ans et permettant de compléter les analyses effectuées par J. Léonard (1975, 1979) lors de précédents congrès de l'AETFAT.

GENRES NOUVEAUX

Au cours des 27 années considérées, 476 genres nouveaux ont été publiés, soit 18 en moyenne par an (Tableau 1).

Entre 1977 et 1979, 39 genres nouveaux ont été décrits, soit 13 en moyenne par an; ils se répartissent dans les familles suivantes.

Amaryllidaceae
(1978): *Saniella*
Amaranthaceae
(1979): *Eriostylos*
Arecaceae
(1978): *Tectiphiala*
Asclepiadaceae
(1978): *Orbeanthus, Orbeopsis, Pachycymbium*
(1979): × *Hoodialluma,* × *Hoodiapelia*
Asteraceae
(1977): *Poecilolepis, Rastrophyllum*
(1978): *Brachytrix, Jeffreya, Notoniopsis, Oreoleysera, Phaneroglossa, Stenops, Xyridopsis*
(1979): *Grananthus*
Chenopodiaceae
(1978): *Sarcocornia*

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TABLEAU 1. Statistique des noms nouveaux au cours de la période 1953–1979.

	Genres Nouveaux	Espèces Nouvelles	Combinaisons Nouvelles	Taxons Infraspécifiques Nouveaux	Total de Noms Nouveaux
1953	29	577	350	221	1.177
1954	23	354	340	140	857
1955	21	426	235	185	867
1956	19	364	216	119	718
1957	16	358	255	102	731
1958	26	452	366	141	985
1959	10	498	239	162	909
1960	22	299	523	124	968
1961	23	476	255	119	873
1962	34	323	374	88	819
1963	17	512	302	148	979
1964	24	358	213	90	685
1965	12	287	311	113	723
1966	19	313	202	90	624
1967	18	266	493	91	868
1968	14	294	173	146	627
1969	9	226	292	79	606
1970	18	245	358	120	741
1971	8	298	270	98	674
1972	12	278	256	85	631
1973	17	274	270	77	638
1974	16	226	267	60	569
1975	9	272	319	105	705
1976	21	133	210	35	399
1977	10	140	166	55	371
1978	22	254	440	83	799
1979	7	202	272	93	574
Total	476	8.705	7.967	2.969	20.117
Moyenne 1953–1979	18	322	295	110	745
Moyenne 1977–1979	13	199	293	77	581

Crassulaceae
(1978): *Tylecodon*
Cyperaceae
(1977): *Marisculus*
(1978): *Kyllingiella*
Iridaceae
(1977): *Barnardiella*
Liliaceae
(1978): *Jodrellia*
Loranthaceae
(1978): *Pedistylis, Vanwykia*
Myoporaceae
(1977): *Ranopisoa*
Orchidaceae
(1977): *Cardiochilos, Holmesia, Summerhayesia*
(1979): *Margelliantha*
Plumbaginaceae
(1979): *Afrolimon*
Poaceae
(1979): *Gossweilerochloa*
Rubiaceae
(1978): *Nichallea, Paracorynanthe, Sericanthe*
Scrophulariaceae
(1977): *Rhabdotosperma, Strobilopsis*
Winteraceae
(1978): *Takhtajania*

ESPÈCES NOUVELLES

Au cours des 27 années considérées, 8.705 espèces nouvelles ont été publiées, soit 322 en moyenne par an. Entre 1977 et 1979, 596 espèces

TABLEAU 2. Nombre d'espèces nouvelles décrites de 1977 à 1979 au sein des diverse familles de phanérogames.

Familles	1977	1978	1979	Total
Acanthaceae	—	6	1	7
Aizoaceae	—	1	2	3
Amaranthaceae	1	2	3	6
Amaryllidaceae	1	3	2	6
Apiaceae	—	2	—	2
Apocynaceae	—	1	1	2
Araceae	1	—	—	1
Araliaceae	1	—	—	1
Arecaceae	—	1	—	1
Asclepiadaceae	9	14	9	32
Asteraceae	7	28	8	43
Balsaminaceae	—	—	24	24
Begoniaceae	—	2	—	2
Bignoniaceae	1	—	—	1
Boraginaceae	—	—	2	2
Brassicaceae	2	1	3	6
Caesalpiniaceae	1	—	—	1
Campanulaceae	—	1	1	2
Caryophyllaceae	2	—	—	2
Chenopodiaceae	—	8	—	8
Commelinaceae	—	1	—	1
Convolvulaceae	—	3	—	3
Crassulaceae	5	9	9	23
Cyperaceae	8	10	—	18
Dichapetalaceae	—	1	2	3
Ebenaceae	—	4	—	4
Erythroxylaceae	1	—	—	1
Euphorbiaceae	5	10	3	18
Fabaceae	—	3	—	3
Geraniaceae	—	—	3	3
Grubbiaceae	1	—	—	1
Iridaceae	12	9	13	34
Lamiaceae	5	4	2	11
Lauraceae	—	—	1	1
Liliaceae	2	30	17	39
Lobeliaceae	—	4	—	4
Loranthaceae	—	3	1	4
Lythraceae	—	2	—	2
Malvaceae	—	—	1	1
Melastomataceae	3	—	11	14
Meliaceae	—	—	1	1
Menispermaceae	2	—	—	2
Mimosaceae	—	3	—	3
Montiniaceae	1	—	—	1
Moraceae	3	—	—	3
Myrsinaceae	6	1	18	25
Myrtaceae	—	—	1	1
Nepenthaceae	1	—	—	1
Nyctaginaceae	—	3	—	3
Oleaceae	—	—	1	1
Orchidaceae	33	22	19	74
Plumbaginaceae	4	—	—	4
Poaceae	4	12	2	18
Podostemaceae	—	1	—	1
Proteaceae	1	3	2	6
Ranunculaceae	—	—	2	2
Rhamnaceae	—	—	1	1
Rubiaceae	8	24	16	48
Rutaceae	—	14	10	24
Sapotaceae	—	2	—	2
Santalaceae	—	—	3	3
Scrophulariaceae	2	—	7	9
Scytopetalaceae	3	—	—	3
Sterculiaceae	—	1	—	1
Stilbaceae	1	—	—	1
Tiliaceae	2	—	—	2
Verbenaceae	1	—	—	1
Zingiberaceae	—	2	—	2
Zygophyllaceae	—	3	—	3

nouvelles ont été décrites, soit 199 en moyenne par an. Le Tableau 2 reprend la répartition des espèces nouvelles décrites durant cette période au sein des diverses familles de phanérogames. Les familles présentant le plus grand nombre d'espèces nouvelles sont les Orchidaceae (74 espèces nouvelles en trois ans), les Rubiaceae (48), les Liliaceae (39), et les Iridaceae (34). Durant le même période (de 1977 à 1979), la répartition des espèces nouvelles au sein des différents pays africains est présentée au Tableau 3. Les pays pour lesquels le plus grand nombre d'espèces nouvelles ont été décrites sont l'Afrique du Sud (avec 172 espèces nouvelles en trois ans), la Tanzanie (104), la Zambie (57), le Kenya (45), et le Zaïre (42).

COMBINAISONS NOUVELLES

Le nombre de combinaisons nouvelles (c'est-à-dire des changements de genre et des changements de rang inférieur au genre) atteint 7.967 pour les 27 années considérées, soit 295 en moyenne par an. Pour la période allant de 1977 à 1979, on observe une valeur moyenne très proche de celle des 27 années; l'écart entre la moyenne annuelle des combinaisons nouvelles (293) et celle des espèces nouvelles (199) y est nettement plus marqué que lors des périodes précédentes. La tendance à modifier les statuts des taxons l'emporte par rapport aux descriptions de nouveaux taxons.

TABLEAU 3. Nombre d'espèces nouvelles, décrites de 1977 à 1979 dans les différents pays africains.

Pays	1977	1978	1979	Total
Afars et Issas	1	—	—	1
Afrique du Sud	33	75	64	172
Aldabra (Archipel)	2	6	1	9
Angola	1	4	4	9
Bénin	—	1	—	1
Botswana	2	1	—	3
Burkina Faso	—	1	—	1
Burundi	6	5	3	14
Centrafricaine (Rép.)	—	2	2	4
Cameroun	9	5	18	32
Congo	3	—	4	7
Côte d'Ivoire	2	1	3	6
Éthiopie	5	7	6	18
Fernando Po (Île)	—	—	1	1
Gabon	7	2	13	22
Ghana	1	1	2	4
Guinée	1	—	1	2
Guinée Bissau	1	1	1	3
Kenya	6	22	17	45
Lesotho	3	6	7	16
Liberia	4	1	4	9
Madagascar	2	2	7	11
Malawi	10	18	3	31
Mali	—	1	—	1
Maurice (Île)	—	3	2	5
Mozambique	3	12	4	19
Namibie	4	13	5	22
Niger	—	1	—	1
Nigeria	1	3	3	7
Ouganda	—	10	4	14
Réunion (Île)	—	2	2	4
Rodrigues (Îles)	—	—	1	1
Rwanda	5	4	5	14
Sierra Leone	1	1	—	2
Somalie	8	4	1	13
Soudan	—	1	2	3
Swaziland	1	3	—	4
Tanzanie	10	55	39	104
Tchad	—	—	1	1
Togo	1	—	1	2
Zaïre	16	19	7	42
Zambie	24	28	5	57
Zimbabwe	14	9	5	28

TAXONS INFRASPÉCIFIQUES NOUVEAUX

En 27 ans, 2.969 taxons infraspécifiques nouveaux ont été publiés, soit 110 en moyenne par an. De 1977 à 1979, 231 taxons infraspécifiques ont été proposés, soit 77 en moyenne par an.

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ENDEMISM AND AFFINITIES OF THE TANZANIAN MONTANE FOREST FLORA[1]

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ABSTRACT

Data are presented which give an estimate of the species richness and species endemism of the Tanzanian montane forest flora. The Tanzanian montane forest flora is estimated to comprise about 2,000 species in approximately 800 genera. Some 25% of these species are endemic to Tanzania, and over 30% are endemic to Tanzania and southeastern Kenya. The majority of the endemics occur in the mountain forests of the eastern part of the country in an area defined as the Eastern Arc mountains. A significant number of species present in the montane forest flora of eastern Tanzania are widespread in the Guineo–Congolian region of Africa or belong to genera characteristic of that region. It is difficult to explain all these affinities by long-distance dispersal, and so a major floristic link must have existed at one time. There are also floristic links with Madagascar, although these are weak in comparison with those of the Guineo–Congolian region.

RÉSUMÉ

Des données sont présentées qui donnent une estimation de la richesse et de l'endemisme de la flore forestière des montagnes de Tanzanie. On estime que cette flore comporte à peu pres 2.000 espèces dans environ 800 genres. 25% des espèces environ sont endémiques à la Tanzanie et plus de 30% sont endémiques à la Tanzanie et au sud est du Kénya. La majorité de ces espèces endémiques se trouvent dans les forêts de montagnes à l'est du pays. Ces montagnes sont définies comme les montagnes de l'Arc Oriental. Un nombre significatif d'espèces présentes dans la flore des forêts de montagnes à l'est de la Tanzanie sont communes dans la région Guinéo-congolaise de l'Afrique ou appartiennent à des genres caracteristiques pour cette région. Il est difficile d'expliquer toutes ces affinités par une dispersion sur de longues distances, et donc un lien floristique important a du exister à une époque. Il y a également des liens floristiques avec le Madagascar, bien que ceux-ci soient faibles comparés à ceux de la région Guinéo-congolaise.

The montane forests of Tanzania have long been recognized as an area of outstanding biological interest, and botanists have been collecting in them for well over a hundred years (Gillett, 1962). In response to the unique nature of the forests, the U.S. National Research Council regarded them as one of the eleven tropical areas of highest priority for biological inventory (National Research Council, 1980), and the World Wildlife Fund have listed them as a priority area in both their Tropical Forests and Plants campaigns.

A flora of the montane forests of Tanzania is needed, and such a project is relatively feasible with the *Flora of Tropical East Africa* (Milne-Redhead et al., 1952 to date) having nearly two-thirds of the families of the FTEA area of Uganda, Kenya, and Tanzania published or in manuscript. An estimate of the flora size is necessary so that the writing of the flora can be effectively planned. In preparing this estimate, I have compiled information on the distribution of the species so that species endemism can be determined and the affinities of the flora assessed.

The decisions relating to the inclusion or exclusion of species for the flora are necessarily subjective, as the flora is intended to be a practical work for people actively involved with the Tanzanian forests. Thus it is important to stress that broad definitions were applied to the inclusion of species, particularly with regard to use of the word montane, which was taken to be forest connected with mountains generally and not the strict ecological definition of a montane forest. This analysis therefore includes forest species

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from lowland to upper montane forests, and from forests with rainfalls of 3,000 mm per year to those receiving less than 1,000 mm.

Brief Description of the Flora Area

Tanzania is a large country, with an area of 939,400 km^2, but much of this is arid, with 96% of the country receiving less than 1,270 mm of annual rain in four years out of five (reliable rain) (Griffiths, 1972) and so too dry to support forest growth. A recent estimate using satellite imagery of the current area of closed moist forest in Tanzania is 16,185 km^2, or 1.85% of the land area (Rodgers et al., 1986), although this is undoubtedly substantially less than would occur naturally due to the rapidly accelerating deforestation by man.

The forested area can be divided into a number of practical subdivisions based on geography and edaphic and floristic factors. The coastal forests have a patchy distribution on the hills, valleys, and islands of the east coast. The Lake Victoria Basin forests occur in the high rainfall areas around Lake Victoria in the extreme northwest of Tanzania. The western mountain forests are on the Mahali and Mbizi mountains. The volcanic forests are on the volcanic mountains of Meru, Kilimanjaro, Hanang, Poroto, and Rungwe. The dry northern forests are found on the nonvolcanic upland areas of Loliondo and Mbulu. The Eastern Arc forests occur on the crystalline block mountains in the east of Tanzania. From north to south these are: Upare, Usambara, Nguu, Nguru, Ukaguru, Uluguru, Rubeho, Malundwe, Uzungwa, Mahenge, Njombe Highlands, and the Matengo Hills.

Phytogeographically (following White, 1983) the Tanzanian forests are part of the Afromontane Region (on mountains over about 1,000 m in altitude), the Zanzibar–Inhambane Regional Mosaic (coastal forests and Eastern Arc forests up to about 1,000 m), and the Lake Victoria Regional Mosaic (Lake Victoria Basin forests).

Flora Limits

For the extraction of data relating to a montane forest flora, some practical limits must be established. In a flora of this nature, which has both an ecological and regional circumscription (being forests and mountains in Tanzania), the flora limits are somewhat difficult to define and a practical compromise needs to be made.

The transition between forest and the surrounding woodland or grassland is quite sharp, probably due to burning, and so it is relatively easy to define which species occur within the forest and which occur outside. The purely forest edge species were excluded, although many of them are of botanical interest. Those species occurring in glades and natural clearings inside the forest were included, as they are obviously part of the forest ecosystem. Some difficulty arises when considering the dry forests of the *Juniperus/Catha* (*Juniperus excelsa* Bieb., Cupressaceae; *Catha edulis* Forsk., Celastraceae) association, as in many areas this vegetation type has an open canopy with high ground cover of grasses and so is rather more like semievergreen woodland (in the sense of Greenway, 1973). These forest types were included largely because they are historically defined as forest, and the transition between the closed canopy dry evergreen forest and the more open type is a continuous gradation.

The political boundary of Tanzania serves as a practical regional limit to the broad flora area, as the *Flora of Tropical East Africa* uses this boundary when presenting distributional data. Unfortunately it does not coincide with floristic units. A number of species with restricted distributions occur in the mountain forests of southeastern Kenya and eastern Tanzania (see below), and these southeastern Kenya forests (notably on the Teita Hills) can be regarded as the northernmost extension of the Eastern Arc forests. It would in fact be logical to include these forests in the final flora.

It is more difficult to define what constitutes a mountain forest, particularly as there is, or was, continuous forest cover from the lowlands at the base of the mountains at 300–400 m to over 2,000 m. The analysis of the montane forests therefore included forests from lowland to upper montane ecological zones. As the lowland forests are Zanzibar–Inhambane and the higher altitude forests are Afromontane, it would be more logical also to include the Zanzibar–Inhambane coastal forests in the final flora.

The forests around Lake Victoria were excluded from the analysis presented here on the grounds that they do not occur in mountainous areas, even though they occur at altitudes of over 1,000 m. Floristically they are a mixture of Afromontane and Guineo–Congolian species (White, 1983) and would probably be quite interesting to include in the final flora as a comparison with the Eastern Arc Forests.

TABLE 1. Families checked that contain at least 30 species in the Tanzanian montane forests, giving number of endemic species and percentage species endemism.

	Species	Genera	Endemics	% Endemism
Annonaceae	37	16	13	35
Balsaminaceae	53	1	27	51
Curcurbitaceae	31	13	2	6
Euphorbiaceae	86	34	16	19
Gesneriaceae	45	3	33	73
Graminae	74	41	2	3
Leguminosae	98	46	18	18
Melastomataceae	37	10	20	54
Moraceae	35	11	3	9
Orchidaceae				
(Data excludes Vandeae.)	124	23	38	31
Rubiaceae	291	62	106	36

Three largest genera represented:
Impatiens (Balsaminaceae); 53 species, 27 endemics.
Polystachya (Orchidaceae); 43 species, 19 endemics.
Psychotria (Rubiaceae); 45 species, 27 endemics.

SOURCE OF INFORMATION

The information used in this analysis was gathered from published and unpublished parts of the *Flora of Tropical East Africa* (FTEA) (Milne-Redhead et al., 1952 to date) and supplemented by study of herbarium material of taxonomically revised families. Of the 200 families occurring in the FTEA area, 135 (67%) were checked for species that occur in the Tanzanian montane forests.

RESULTS

Of the 135 families checked, 93 have species in the Tanzanian montane forest. Of the total number of families occurring in the FTEA area, 139 are actually represented in the Tanzanian montane forests (data derived from literature and herbarium material), so 67% of forest families were checked for this analysis. In the families checked, there were 1,301 species in 490 genera occurring in Tanzanian montane forest. In order to obtain an estimate for the whole flora, these figures were multiplied by 1/0.67, using the assumption that the remaining unchecked families contained the same proportion of forest species and were of a similar average size to the checked families. Of the remaining unchecked families, a number are well represented in the forests—for example the Acanthaceae, Celastraceae and the Apocyanaceae—and so this assumption will not suffer from the problem of all the remaining families being monotypic. The estimated total montane forest flora size is therefore 2,173 species in 818 genera.

ENDEMISM

The Tanzanian montane forests contain a remarkably high number of endemics. Of those families checked, 49 contained species endemic to Tanzania (53% of forest families). Of the genera checked, 126 contained endemic species (26% of forest genera). Of the species checked, there were 326 endemics (25% of forest species). If species occurring in Tanzanian montane forests and extending into southeast Kenya (the K7 area of the *Flora of Tropical East Africa*) are treated as endemics, then there are 380 endemic species (30% of forest species). Thus the total estimated number of endemic species in the montane forests of Tanzania is approximately 540, and those endemic to Tanzania and southeastern Kenya is 650.

Table 1 shows those families checked that have at least 30 species in the Tanzanian montane forests. Of the large families that are well represented in the forest, Acanthaceae, Apocyanaceae, and Celastraceae were not checked in this analysis. Table 1 also shows the three largest genera represented and the number of species they contain in the forest for those families checked.

The endemics can be localized within Tanzania by reference to the flora areas used to divide up the *Flora of Tropical East Africa*. These

TABLE 2. Occurrences of endemic Tanzanian montane forest species in different *Flora of Tropical East Africa* areas. The number and percentage of total occurrences of the species recorded in each area is given. 89% of total occurrences are in the T3, T6, and T7 areas, which contain the Eastern Arc mountains.

FTEA Area	Occurrences	% Occurrences
T1	1	0.2
T2	27	6
T3	150	33
T4	9	2
T5	2	0.4
T6	200	44
T7	55	12
T8	11	2
Z	1	0.2
P	1	0.2
Total	457	

flora areas (T1 to T8, Zanzibar and Pemba) correspond to the old administrative boundaries within Tanzania when it was a British protectorate. Table 2 gives the number of occurrences of Tanzanian montane forest species endemic to Tanzania in the different Tanzanian flora areas for those families checked. The T3, T6, and T7 areas include the Eastern Arc mountains and contain the largest number of endemics. This is in marked contrast to the T2 area, which contains some recent volcanic mountains and dry northern forests. Another interesting point is that the T1 area, which contains the Lake Victoria Basin forests (not included in this analysis) possesses very few of the endemics that occur in the east of the country. This demonstrates the unique nature of the eastern Tanzanian montane forests.

The high degree of endemism is not restricted to species, as there are at least 11 genera endemic to the forests of the Eastern Arc mountains (Table 3).

TABLE 3. Endemic or near endemic genera of the montane forests of eastern Tanzania.

Cephalosphaera Warb. (Myristicaceae)—1 species eastern Tanzania.
Dionychastrum A. & R. Fernandes (Melastomataceae)—1 species eastern Tanzania.
Dolichometra K. Schum. (Rubiaceae)—1 species eastern Tanzania.
Englerodendron Harms. (Leguminosae: Caesalpinoideae)—1 species eastern Tanzania.
Linnaeopsis Engl. (Gesneriaceae)—4 species eastern Tanzania.
Platypterocarpus Dunkley & Brenan (Celastraceae)—1 species eastern Tanzania.
Pseudonesohedyotis Tennant (Rubiaceae)—1 species eastern Tanzania.
Rhipidiantha Bremek. (Rubiaceae)—1 species eastern Tanzania.
Saintpaulia H. Wendl. (Gesneriaceae)—20 species eastern Tanzania and southeastern Kenya.
Zimmermannia Pax (Euphorbiaceae)—7 species eastern Tanzania, southeastern Kenya, and Madagascar.

Gen. nov. aff. *Sideroxylon* in ed. sensu FTEA (Sapotaceae)—1 species eastern Tanzania.

TABLE 4. Affinities of the Tanzanian montane forest flora. Percentage occurrence of species in regions outside Tanzania.

30% occur in countries to the west of Tanzania.
12% occur in countries to the north of Tanzania.
26% occur in countries to the south of Tanzania.
32% are widespread (i.e., occur to north, west, and south).

AFFINITIES OF THE FOREST FLORA

The distribution outside Tanzania of those Tanzanian montane forest species in the families checked was assessed by determining whether they occurred in countries to the north, south, or west, or were widespread in that they occurred in all these directions. The percentage of occurrences in each direction is indicated in Table 4. The main affinities of the flora are to the west and south, rather than the north.

The Eastern Arc forests possess a number of species and genera whose distribution is predominantly Guineo–Congolian (Faden, 1974; Hamilton, 1976; Morton, 1972; White, 1983) and which have a marked disjunction (Table 5).

To a lesser extent the Tanzanian montane forest flora has affinities with Madagascar, both at the species and generic level. This is restricted to a few, but nonetheless interesting, examples (Table 6). Further examples of bryophytes common to Tanzania and Madagascar are given by Pócs (1975). A general discussion of the affinities of the Madagascan flora with east and southern Africa is given by Leroy (1978). The genus *Adenoplusia* Radlk., once thought to be endemic to the Eastern Arc forests (Brenan, 1978), has now been sunk into *Buddleja axillaris* (Radlk.) Leeuwenberg (Leeuwenberg, 1979). Some further links with Madagascar may appear as the knowledge of African taxonomy increases.

TABLE 5. Some species and genera that are disjunct between the Guineo–Congolian region and the Eastern Arc forests.

Species of genera predominantly Guineo–Congolian:
Anonidium usambarense R. E. Fr. (Annonaceae)
Enantia kummeriae Engl. & Diels (Annonaceae)
Isolona heinsenii Engl. & Diels (Annonaceae)
Polyceratocarpus scheffleri Engl. & Diels (Annonaceae)
Mammea usambarensis Verdc. (Guttiferae)
Octoknema orientalis Mildbr. (Olacaceae)
Oxystigma msoo Harms (Leguminosae: Caesalpinoideae)
Tessmannia densiflora Harms (Leguminosae: Caesalpinoideae)
Tessmannia martiniana Harms (Leguminosae: Caesalpinoideae)
Uvariopsis bisexualis Verdc. (Annonaceae)
Species Guineo–Congolian in distribution, but which have subspecies that occur only in the Eastern Arc forests:
Greenwayodendron suaveolens (Engl. & Diels) Verdc. subsp. *usambaricum* Verdc. (Annonaceae)
Pterocarpus mildbraedii Harms subsp. *usambarensis* (Verdc.) Polhill (Leguminosae: Papilionoideae)
Magnistipula butayei De Wild. subsp. *greenwayi* (Brenan) F. White (Chrysobalanaceae)
Species that are Guineo-Congolian except for occurrences in the Eastern Arc forests:
Calvoa orientalis Taub. (Melastomataceae)
Cincinnobotrys oreophila Gilg (Melastomataceae)
Crotonogynopsis usambarica Pax (Euphorbiaceae)
Chrysophyllum perpulchrum Hutch. & Daz. (Sapotaceae)
Cyrtococcum chaetophoron (Roem. & Schult.) Dandy (Graminae)
Dioscoreophyllum volkensii Engl. (Menispermaceae)
Flabellariopsis acuminata (Engl.) Wilczek (Malpigiaceae)
Hetaeria heterosepala (Reichb. f.) Summerh. (Orchidaceae)
Ipomea urbaniana (Dammer) Hall. f. (Convolvulaceae)
Isolona hexaloba (Pierre) Engl. & Diels (Annonaceae)
Leptaulis holstii (Engl.) Engl. (Icacinaceae)
Olax gambecola Baill. (Olacaceae)
Puelia olyriforis (Franch.) W. D. Clayton (Graminae)
Pyrenacantha vogeliana Baill. (Icacinaceae)
Raphidiocystis chrysocoma (Schumach.) C. Jeffrey (Cucurbitaceae)
Rinorea subintergrifolia (Beauv.) Kuntze (Violaceae)
Saintpauliopsis lebrunii Staner (Acanthaceae)
Schefflerodendron usambarense Harms (Leguminosae: Papilionoideae)
Uapaca paludosa (Euphorbiaceae)

TABLE 6. Some floristic affinities between the Tanzanian montane forest flora and Madagascar.

Species of genera restricted to Madagascar (and Islands) and eastern Africa, including eastern Tanzania:
Aphloia theiformis (Vahl) Benn. (Flacourtiaceae)
Danais xanthorrhoea (K. Schum.) Bremek. (Rubiaceae)
Humbertochloa greenwayi C. E. Hubbard (Graminae)
Ludia mauritiana Gmelin (Flacourtiaceae)
Seychellaria africana Vollesen (Triuridaceae)
Sparmannia ricinocarpa (Eckl. & Zeyh.) O. Kuntze (Tiliaceae)
Zimmermannia grandiflora Verdc. (Euphorbiaceae)
Species occurring in Madagascar and eastern Tanzania:
Buddleja axillaris (Radlk.) Leeuwenberg (Loganiaceae)
Illigera madagascariensis Perrier (Hernandiaceae)
Lepidiotrichilia volkensii (Gurke) Leroy (Meliaceae)
Leptochloa squarrosa Pilg. (Graminae)
Microcoelia physophora (Reichb. f.) (Orchidaceae)
Panicum mitopus K. Schum. (Graminae)
Rinorea squamosa (Tul.), Baill. (Violaceae)
Zehneria emirnensis (Bak.) Keraudren (Cucurbitaceae)

DISCUSSION

The montane forests of Tanzania, as defined in a broad sense, contain a remarkable number of endemic species and genera. The uniqueness of the flora can be demonstrated by comparison of the Tanzanian montane forests with other areas in Africa (Brenan, 1978). The estimated total flora size of the Tanzanian montane forests is 2,173 species in 818 genera in about 15,000 km^2. The estimated total flora size for tropical Africa is 30,000 species in 2,497 genera in 20 million km^2. Thus the Tanzanian forests contain 33% of the genera and 7% of the species of tropical Africa in 0.075% of the area. The forests also contain about as many endemic plant species as the estimated number of individual country endemics (Brenan, 1978) of Kenya, Malawi, Mozambique, and Uganda combined (estimated at about 580).

Most of the endemic taxa occur in the Eastern Arc mountains, and it is interesting to note that these mountains show strong floristic similarities to each other and not to adjacent recent volcanic mountains. This may be due to edaphic factors in that volcanic-derived soil is rather different than that on the crystalline Eastern Arc. Or it

TABLE 7. Some species endemic to the rain shadow area to the west of the Uzungwa and Rubeho Mountains (J. B. Gillett & S. Holmes, pers. comm.).

Commiphora acuminata Mattick (Burseraceae)
C. ruahensis Mattick (Burseraceae)
Cordyla densiflora Milne-Redh. (Leguminosae: Caesalpinioideae)
Erythrina greenwayi Verdc. (Leguminosae: Papilionoideae)
Euphorbia dumeticola Bally & S. Carter (Euphorbiaceae)
E. proballyana Leach (Euphorbiaceae)
Monadenium arborescens Bally (Euphorbiaceae)
M. magnificum E. A. Bruce (Euphorbiaceae)
Ormocarpum flavum Gillett (Leguminosae: Papilionoideae)
Peterodendron ovatum (Sleumer) Sleumer (Flacourtiaceae: monotypic endemic genus)
Sesbania paucisemina Gillett (Leguminosae: Papilionoideae)

may be due to the fact that most of the forest on the volcanic mountains below 1,800 m has long since been destroyed for cultivation on the fertile wet slopes. Alternatively, the rich flora present on the Eastern Arc mountains, which have probably been in existence since the Cretaceous (Sowerbutts, 1972), has not yet fully dispersed to the volcanoes of Kilimanjaro and Meru, which were not in existence prior to the beginning of the Quaternary (Saggerson, 1972). A similar suggestion is made by Pócs (1975) to explain a corresponding distribution of bryophytes.

It seems highly probable that the Eastern Arc mountains have had forest cover at least since the Miocene, some 25 million years ago, and there are a number of characteristics of the current forest flora that appear to confirm this. One possible indication of an ancient flora is the ratio of species to genera, so that a small species/genus ratio derived from many small genera may indicate a more ancient flora which is no longer actively speciating; whereas a large species/genus ratio, which results from a few large genera, suggests a flora currently in the process of evolving (Stebbins, 1972). The Tanzanian forests have a low species to genus ratio of 2.6, which is comparable to that of other presumed ancient ecosystems in Africa, such as the Namib. Here the species/genus ratio of 2.9 is thought to demonstrate the ancient nature of the flora (Robinson, 1978). However, it is worth noting that the flora of the British Isles has a species to genus ratio of 2.7 (1,443 species and 545 genera, excluding apomictic microspecies; Dandy, 1958), yet it has a predominantly recently arrived flora dating from the last glacial epoch. Thus the species/genus ratio is probably not a good general indicator of flora age.

Rather better evidence for the ancient nature of the forests comes from the strong links they have with the west African Guineo–Congolian forests. For the purposes of this discussion, the definition of east and west Africa is geographical and biological rather than political. Thus Uganda is regarded as west African, as it contains the easterly extension of the Guineo–Congolian region, although it is politically part of East Africa. Similarly, east Africa may be defined as that area to the east of the southern extension of the Somalia–Masai region. The floristic connection between east and west African forests was severed by the uplifting of the central Tanzanian plateau and desiccation of the African continent during the late Oligocene to early Miocene (Axelrod & Raven, 1978). Since that time it is very unlikely that there has been any major exchange of moist forest plant genetic material between east and west Africa. But, as has been demonstrated, there is a strong link between east and west Africa (Tables 4, 5).

An example of the lack of genetic exchange between east and west Africa is *Maesopsis eminii* Engl. (Rhamnaceae), which is Guineo–Congolian in distribution and readily dispersed by hornbills. It has been introduced as a plantation timber tree into the Eastern Arc forests, where it grows well enough to have become naturalized in many places. Its natural range is from Lake Victoria westward to Liberia, northward to the Imatongs, and south to small forest patches south of the river Cuanza in Angola (White & Werger, 1978), where it is either remnant from an earlier extension in the area of the Guineo–Congolian forests or has dispersed through the isolated areas of cloud forests to the north (the Dembos forests). However, it has failed to reach the Eastern Arc forests naturally, either as a result of an extension of the area of the Guineo–Congolian forests or by long-distance dispersal. This testifies to the isolation of the Eastern Arc forests from recent Guineo–Congolian influence.

Thus, between east and west Africa there has been a very marked, ancient, arid corridor across which forest plants have difficulty in dispersing. This arid corridor was probably more extensive at one time, as evidenced by disjunctions between northeast and southwest African arid land species (Verdcourt, 1969; Monod, 1971; Winterbottom, 1978). There have been marked pe-

riods of aridity in the last 40,000 years (Hamilton, 1982), which may account for these disjunctions. The central Tanzanian arid area is almost certainly very old, as it is created by the rainshadow of the Eastern Arc mountains and is characterized by some notable endemic species (Table 7). Similar arid areas of endemism occur on the Somalia/Kenya/Ethiopia border (M. G. Gilbert, pers. comm.).

Some caution is needed, however, when relating plant distribution to time, as pointed out by Hall & Swaine (1981), who state that "Distributional data are of only limited value in assessing past climatic change because they give no indication of time scale." In the 25 million years since the Miocene uplifts and postulated desiccation of the African continent, it is quite possible that dispersal of plant species between east and west Africa has occurred. For example, the major climatic events may have determined the main distribution patterns, and then subsequent, more minor climatic changes have permitted dispersal to occur by means of "stepping stones" during pluvial periods when the forest would have been more extensive than at present, as suggested by Morton (1972). Such dispersal may account for the present-day similarities between the east and west floras, although if such readily dispersed plants as *Maesopsis* cannot cross the east-west gap, then it is perhaps unlikely that many other plants have done so, particularly those with large seeds.

The affinities of the Tanzanian forests to the south are largely due to similarities with the Malawi forests, discussed by Chapman & White (1970). The Malawi mountains are geologically similar to those of the Eastern Arc, and there are faunal connections (Moreau, 1966). The Afromontane element of the Eastern Arc forests has been divided in the past into southern Uluguru–Malanje (from the Nguru southward) and northern Usambara–Imatong (from Usambara northward) sections (White, 1978). Although it appears that there is objective confirmation of this division through a quantitative analysis of plant species distribution (Denys, 1980), in fact this objective study was based on a small sample of taxa with inaccurate distributional records, and so was not suitable for fine-scale division of phytogeographical regions. It is more useful to consider the Eastern Arc as a floristic unit with gradual impoverishment southward into the Malawian forests.

Although there are strong similarities between the Eastern Arc and the Malawi forests, their environments are probably slightly different, which will determine which species can grow in the forests even if they can disperse between the mountains. For example the ferns *Bolbitis auriculata* (Lam.) Alston, *B. acrostichoides* (Swartz) Ching, and *B. gemmifera* (Hieron) C. Chr. (Lomariopsidaceae) have a tropical African distribution from east to west Africa but do not occur below 10°S on continental Africa (Hennipman, 1977), although they must be readily dispersed by spores. As haploid fern gametophytes are regarded as being particularly sensitive to environment (Parris, 1985), then fern distribution must depend on fairly narrow environmental parameters. This indicates an environmental difference between the tropical African forests and those south of 10°S. Some ferns are less sensitive; for example, *Bolbitis heudelotii* (Bory ex Fee) Alston has a tropical African distribution but extends south into Malawi and north into Ethiopia.

Madagascar separated from east Africa 80–100 million years ago (Axelrod & Raven, 1978) and has a distinctive flora with affinities to east Africa (Pócs, 1975; Leroy, 1978; Wild, 1975; Vollesen, 1980). Although some of the affinities between Madagascar and east Africa may predate the breakup of Gondwanaland, it is also likely that some of them result from long-distance dispersal, as many of the species and genera common to eastern Tanzania and Madagascar have potentially readily dispersed fruits.

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SUCCESSION ON THE COASTAL DUNES AND DUNE SLACKS AT KLEINEMONDE, EASTERN CAPE, SOUTH AFRICA[1]

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Abstract

Experimental studies undertaken 1980–1985 on dune slack species and our observations and interpretative climatic data have provided us with the following insights into dune plant succession. *Scaevola plumieri,* along with other species, are pioneers of the foredunes. In wet slacks, the sedge *Scirpus nodosus* invades by means of wind-borne seeds; whereas in the drier margins, *Arctotheca populifolia* and *Sporobolus virginicus* are the major pioneers. Once *S. nodosus* has become established, *Juncus kraussii* appears, suggesting that slacks dominated by this rush are older and drier. In the last two years a few shrubs characteristic of older slacks and coastal scrub such as *Rhus crenata* were recorded. Climatic factors, especially rainfall and wind, appear to be the major factors affecting natural plant succession in this ecosystem. A decline in rainfall and available soil moisture in more recent years has resulted in a decline of plant abundance in the slacks as dry wind-borne sand has buried the vegetation. The slack vegetation appears to migrate in an easterly direction as the predominant westerly winds move large amounts of sand and bury the plants on the western side of the slacks. Unless higher rainfall conditions return, succession to the climax coastal scrub will not be attained.

Résumé

Des études expérimentales menées de 1980 à 1985 sur une espèce d'arrière-dunes de même que nos observations et des données climatiques nous ont permis d'obtenir les renseignements suivants sur la succession de plantes dans les dunes. *Scaevola plumieri,* parellèlement à d'autres espèces, est l'espèce pionnière des avant-dunes. Dans des endroits humides, *Scirpus nodosus* envahit ce territoire au moyen de graines portées par le vent, tandis que sur les bords plus arides, *Arctotheca populifolia* et *Sporobolus virginicus* sont les espèces pionnières les plus importantes. Une fois que *S. nodosus* s'est établie *Juncus kraussii* apparaît, ce que permet de suggérer que les pentes dominées par cette espèce sont plus anciennes et plus sèches. Ces deux dernières années quelques buissons caracteristiques de dunes plus anciennes et des fourés côtiers tels que *Rhus crenata* ont été répertoriées. Des facteurs climatiques, en particulier les précipitations et le vent, semblent être les facteurs qui influencent le plus la succession naturelle de plantes dans cet écosystème. Une baisse de précipitation et une diminution de l'humidité du sol ces dernières années a entraîné une baisse du nombre de plantes dans les dunes alors même qu'un sable sec transporté par le vent recouvrait la végétation. La végétation des dunes semble migrer vers l'est alors que les vents d'ouest prédominants transportent de larges quantités de sable et enterrent les plantes sur le côté occidental des dunes. A moins que les précipitations ne s'accroissent, il n'y aura pas de succession au stade climatique de fouré côtier.

Extensive dune systems exist along the Eastern Cape coast, many of which are not colonized by vegetation apart from dune scrub species that occur well above the high-water level. At Kleinemonde there is a portion of the dune field that is sheltered from the harsh coastal environment and the succession of plants on the dunes and dune slacks is more apparent. The vegetation of the area was described by Lubke (1983), who noted a greater variety of species in the dune slacks than on the mobile foredunes.

Following initial descriptions of the coastal communities, we studied the dune slack vegetation in more detail to investigate how environmental factors affect the distribution of plants, particularly *Scirpus nodosus,* within the slack. We noted that sand movement is not as marked in the slacks as in surrounding dune regions (Lubke & Avis, 1982a) as the sand is removed to a level at which it is immobilized by groundwater (Willis et al., 1959). Only during severe storms is sand deposited in the dune slacks. Oth-

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er factors investigated, such as available soil moisture, soil salinity and pH, and intensity of sea spray, were also found to play a role in confining the distribution of dune slack species to these sites. In particular, salt spray appeared to be an important growth-limiting factor for *Scirpus nodosus* seedlings (Lubke & Avis, 1982b).

Initial observations made on the succession of plants in the dune slack indicated that *Scirpus nodosus* was the primary colonizer of moist slacks (Lubke & Avis, 1982a). Seedlings of these plants were transplanted at various localities in the dune field, and it was found that sand movement caused early death of the seedlings (Avis & Lubke, 1985), thus showing that they are restricted to the slacks where little sand movement occurs.

The dune profile surveyed in 1980 (Lubke, 1983) and the dune slack that was mapped in 1981 (Avis, 1981) were permanently marked, and we repeated surveys annually in order to monitor vegetational changes. The aim of this paper is to present the results of our surveys, synthesize our existing knowledge on the vegetation of the dune system, and explain what vegetational and environmental changes took place. We are also able to provide a conceptual model of succession in the dunes and dune slacks that applies to this whole coastline.

Study Area

The dune system studied occurs at Kleinemonde, about 12 km east of Port Alfred (27°4′E, 33°33′S). The dune slack was formed within the parabolic dunes, which are concave to the direction of the prevailing west and southwest winds. The slack is partially protected from winds by fairly large dunes to the east and west and a large dune on the southern or seaward side. It is a wet slack (Ranwell, 1972) and has a greater diversity of species and abundance of plants than do most of the drier dune slacks along this section of the coast (Lubke, 1983). The dune transect passed immediately to the west of the dune slack that was studied in detail. This transect line was most representative of foredune, dune slack, and rear dune vegetation of the region at the time of the initial survey in 1980 (Lubke, 1983).

Methods

Climatic Data

Climatic data are recorded at the Great Fish Point Lighthouse weather station, 2 km east of the study site and at an altitude of 73 m. Rainfall and maximum and minimum temperatures were taken from published records for the period January 1979 to December 1984 (Weather Bureau, 1984). Wind speed and direction were taken from records at the lighthouse for April–July 1983 for our previous study (Avis & Lubke, 1985) as the nearest published records are for East London (Schulze, 1980).

Salt Spray

The distribution of wind-borne salt along the dune profile was measured with salt traps consisting of 20 cm^2 pieces of cheesecloth stretched onto light wooden frames by means of thumbtacks (Oosting & Billings, 1942; Lubke & Avis, 1982a). Three traps were set up facing the prevailing winds at sites 1, 2, 4, and 5 (Fig. 6) at noon on 12 September 1981 when a strong southwesterly wind was blowing. Salt traps were set up at sites 1 and 3–8 at noon on 1 September 1983 when a strong easterly wind was blowing. In each case, after 24 hours the cheesecloth was removed and 1 dm^2 cut out and stored in a glass vial. The cheesecloth pieces were soaked in 200 ml deionized water for 10 minutes and the amount of chloride present was measured using an EIL chloride electrode and a Labotec Specific Ion Meter (Model 17). The wind speed and direction was measured at each site when the traps were set up and when removed.

Soil Factors

Soil samples were taken from the surface 5 cm at the center of quadrats 1–20 in the dune slack (Fig. 8); pH, conductivity, and moisture content were measured for each sample following the methods of Lubke (1983). Using a soil auger, the depth from the soil surface to the water table was measured in each quadrat to a maximum of 1 m. In the moist center of the sample site (quadrats 11, 12, and 20) water samples were taken and pH and conductivity of the water were measured.

Vegetation Sampling and Analysis

In July 1980 a 1 m^2 belt transect was sampled from the high-water mark to the edge of the coastal scrub. The transect was positioned to pass through the most vegetated region of the dune field. Plant height, percentage aerial cover, and number of rooted shoots of each species were

recorded. An Abney level was used to measure the slope along the transect line. The transect was resampled in January 1985 along the same position, although the slack vegetation was no longer well represented in this area. The same parameters were recorded, and these data were used to construct the two profile diagrams (Figs. 5, 6).

The dune slack vegetation was initially triangular in shape. Three reference points, A, B, and C (Fig. 8), were permanently marked with rock cairns in September 1981. A string grid was placed over the sample area and the vegetation plotted to scale on a map. Identical quadrat positions could be relocated each time the area was resurveyed.

Twenty 1 m^2 quadrats were located at the bottom left of each large quadrat (Fig. 8), where quantitative vegetational data and soil samples could be taken. Quadrats 9, 13, 16, 18, and 19 lay at the edge of the sample area and were not sampled for vegetation. The number of individuals of each species was recorded in each quadrat. Initially the *Scirpus nodosus* population consisted of many plants of different sizes; plants were therefore enumerated in three height classes: <5 cm, 5–30 cm, and mature plants >30 cm.

The initial dune slack survey was made in spring–September 1981, but successive studies were made in summer–February 1983, January 1984, and February 1985. The results were recorded as community maps showing the distribution of all the species in the community.

Using the quadrat count data, the mean density (plants m^{-2}) and percentage frequency were calculated for each species. The total density of plants in all the quadrats was obtained by summation and the relative density of each species determined by expressing total density of each species as a percentage of this total. Thus a quantitative comparison of abundance of all species in the dune slack could be illustrated in the form of pie charts for each sample date (Fig. 11).

A comparison of species diversity in the dune slack was made at each time of sampling by calculating a diversity index. This is a more reliable measure of diversity than number of species or species richness, as the diversity index takes into account the abundance or numbers of individuals in the sample (Brower & Zar, 1984). We used Simpson's index of diversity (Ds) and dominance (ℓ) to show changes in diversity and dominance respectively (Simpson, 1949). As a comparison, the Shannon index (H′) to base 10 was also calculated (Shannon, 1948).

Results

Climatic data

Mean monthly temperatures and total monthly rainfalls were plotted for the period July 1979 to December 1984, and for the total period of available records in the form of Walter & Lieth (1967) climatic diagrams (Fig. 1). The dates of vegetation sampling were also recorded on this figure. Table 1 summarizes the mean annual temperature and the total rainfall. As with most summer rainfall areas of southern Africa, there is evidence of a drier cycle in the 1980s as was predicted by the Tyson & Dyer (1975) model. During this period there is a predominance of arid conditions. Even within the dry cycle, wetter years are evident, as seen in 1981 when warm, moist periods and wet periods are more frequent. There is a great variation in rainfall, with almost any month being either excessively drier or wetter than the mean. Temperatures are not extreme, fluctuating around a mean of 18°C, but local temperature conditions, dependent on aspect and exposure, are more critical in the dune environment. Rapid changes have also been recorded due to berg wind conditions (Lubke, 1983). These climatic factors appear to be particularly important in the initial stages of dune slack succession, as pioneer species invade when conditions are most favorable for germination and growth of seedlings.

Wind direction along this section of the coast is predominantly from the southwest and west during the winter months and from the northeast and southwest in the summer months (Fig. 2B). Severe winds may be recorded during storm periods from either the westerly or easterly direction as was evident during the period when we transplanted *Scirpus nodosus* seedlings on the dunes (Fig. 2A). The movement of sand from west to east during a few days of storm conditions in July 1983 was considerable (Avis & Lubke, 1985), as seen in the photographs of the line transect (Fig. 7). The net result of the extremely windy conditions on this section of the coast is the movement of sand mainly towards the east in the winter months and a reversal of direction in the summer months, when easterly winds are more frequent. We have recorded the advance of a western dune onto the slack at a rate of about 3 m per year over the three-year period. McLachlan et al. (1987) also noted an easterly or northeasterly movement of dunes at a rate of 7 m per year in the Alexandria dune fields.

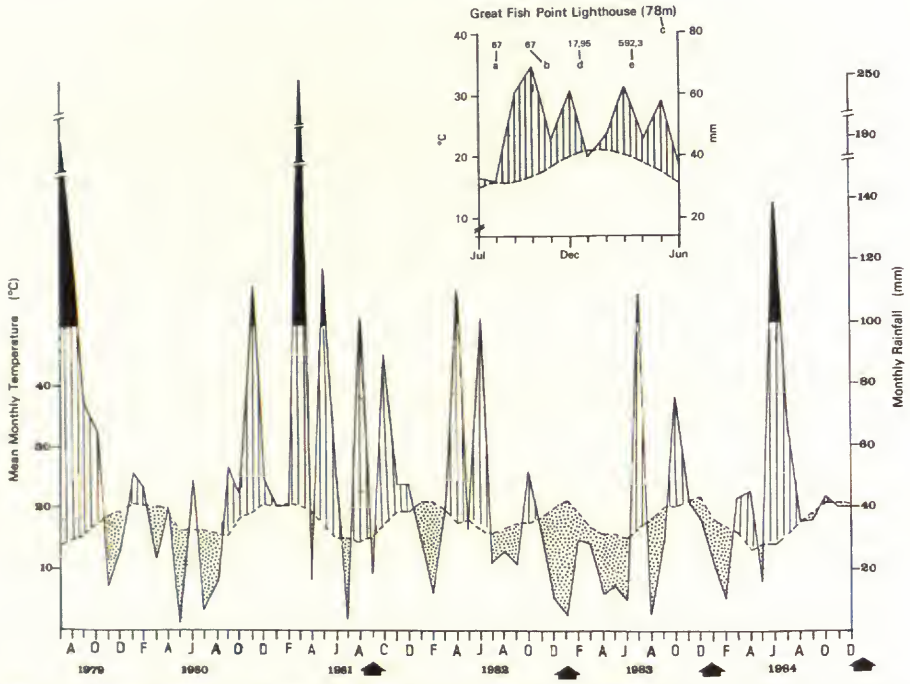

FIGURE 1. Climate diagram for the Great Fish Point Lighthouse weather station for the period 1979–1984. The inset summarizes the mean values for the total period of the records. a = number of years of temperature records, b = number of years of precipitation records, c = altitude, d = mean annual temperature, e = mean annual precipitation, – – – rainfall, — temperature. Vertical lines indicate humid periods, stippling indicates arid periods, and shaded areas indicate a precipitation greater than 100 mm. Arrows show the date of vegetation sampling.

SALT SPRAY

The amount of salt spray recorded at each site was calculated as Cl^- concentration (Lubke & Avis, 1982a; Avis & Lubke, 1985) but is shown here as the percentage of the total Cl^- intercepted at each site (Table 2). Depending on the wind speed, different amounts of salt will be trapped; thus the distribution of salt spray along the line transect is a more useful comparative measure. On both occasions the greatest percentage of wind-borne salt is intercepted on the foredunes (sites 1 and 2, Fig. 6). Sites 3–7, which are in the slack or protected by the dunes, intercept less salt spray. The vegetation also intercepts some of the wind-borne salt, as McAtee & Lynn Drawe (1981) observed on the dunes along the Gulf coast of Texas. However, with an easterly wind, the slack at site 4 is not well protected and a higher percentage of the total salt spray was intercepted here when the second readings were made in September 1983. Wind speed is usually a good indicator of the proportion of salt that will be intercepted; but in September 1983, when our readings were taken, the wind had dropped considerably from about 13 m sec.$^{-1}$ on 1 September to about 4 m sec.$^{-1}$ on 2 September, and it had

TABLE 1. Mean annual temperature and total annual rainfall for the years 1979–1984 and for the total 67-year period of records at Great Fish Point Lighthouse.

	1979	1980	1981	1982	1983	1984	67-Year Period
Mean annual temperature (°C)	17.8	18.2	17.9	18.0	18.4	18.2	17.95
Total annual rainfall (mm)	748.8	495.5	903.6	493.6	399.6	523.2	592.3

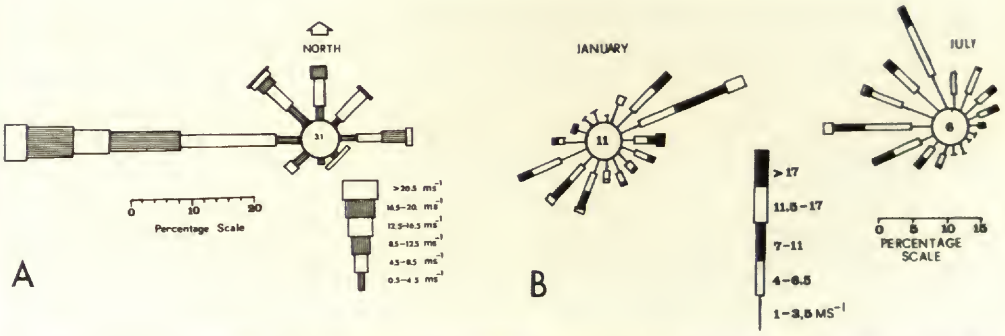

FIGURE 2.—A. Wind rose for Great Fish Point Lighthouse for the period April to July 1983. Data from actual records.—B. Wind roses for East London. Data from Schulze (1980).

also changed direction to the south (Avis & Lubke, 1985). Consequently, a high reading at site 4 indicated that during most of the period that the traps were in situ the wind was gusting from the east. At site 8, more than 200 m from the sea, a large amount of salt was intercepted, as wind is deflected upwards by the foredunes and salt is thus deposited at the next obstacle, the rear dune, as was also observed by Oosting & Billings (1942). Any winds exceeding 7 m sec.$^{-1}$ have a sufficient velocity to carry salt spray inland (Boyce, 1954); thus significant quantities of salt spray can be carried inland on this section of the coast, since wind speeds often exceed this velocity (Fig. 2).

Wind-borne salt, when deposited on the leaves, is detrimental to the growth of *Scirpus nodosus* (Lubke & Avis, 1982b). Salt may also accumulate in the sand, thus retarding root growth or affecting the general metabolism of the plant when absorbed. Preliminary studies by Allam (1984) were made on the effect of salt spray on other species in this area. Donnelly & Pammenter (1983) reported that salt spray was not an important factor controlling vegetation distribution in the Natal dunes. It is likely that many of the dune slack species are confined to this region because of salt spray, and this would explain the greater diversity and abundance of plants in the slack as compared with the dunes.

SOIL FACTORS

In our 1981 study on *Scirpus nodosus* (Lubke & Avis, 1982a), we related the distribution of the plants to the soil factors. Data were collected at grid points and along the margins of the study area, and isolines of pH, percentage moisture, and conductivity were plotted on a map (Fig. 3).

We found that there was a significant negative correlation between pH and conductivity ($r = -0.739$, $P < 0.001$) and pH and moisture ($r =$

TABLE 2. Wind speed and amount of chloride intercepted at various sites along the transect. The location of the sites is shown in Figure 6.

		1981		1983	
Locality	Site Number	% of Total Cl^- Intercepted	Wind Speed at 12 M. on Sept. 13, 1981 (m sec.$^{-1}$)	% of Total Cl^- Intercepted	Wind Speed at 3:00 P.M. on Sept. 2, 1983 (m sec.$^{-1}$)
Foredune	1	71.6	2.87	43.40	3.6
	2	24.3	2.23		
Dune slacks	3	3.9	1.60	3.95	0.4
	4	0.17	0.92	23.50	0.4
	5			1.37	0
	6			3.67	0
	7			0.08	0.4
Rear dune	8			24.0	0.6

FIGURE 3. Map of the dune slack showing the distribution of *Scirpus nodosus* plants of the following isolines: —A. Soil pH.—B. Percentage soil moisture.—C. Soil conductivity.

-0.865, $P < 0.001$), and a positive association between moisture and conductivity ($r = 0.607$, $P < 0.01$). The isolines all followed the same trend, with different regions of the slack demarcated by these lines. A moist central region with a low pH and high conductivity was detected. Moving outwards through inner to outer and marginal regions of the slack, there was a decrease in moisture content and conductivity and an increase in pH (Table 3).

The most significant soil factor in the dune slack is the water content. Germination of *Scirpus nodosus* seeds is probably triggered by the amount of moisture available in the soil and subsequent growth, and development is dependent on the available water supply. The lower lying regions within the dune slack will accumulate greater amounts of rainwater, and during the period prior to the first sample date of September 1981, adequate rainfall resulted in a soil moisture buildup. At this time the water table was also found to be much closer to the surface (Lubke & Avis, 1982a).

We concluded (Lubke & Avis, 1982a) that a higher conductivity was recorded in the center of the slack, as salts are leached from the surrounding sands and accumulate in the lower lying regions. It is unlikely that the slight increase in salinity, as reflected by the conductivity (Fig. 3), had any bearing on the establishment of seedlings of *Scirpus nodosus*. Likewise the pH isolines reflect a relationship between water content and pH and have no bearing on the growth of plants in the different regions of the slack.

Subsequent measurements of soil factors showed no marked relationship with the distri-

TABLE 3. Soil and water factors (mean ± standard error) measured in the dune slack over a four-year period.

		Region of the Slack and Corresponding Quadrat Numbers			
	Year	Central 7, 11, 15 & 20	Inner 6, 8, 12 & 13	Outer 2, 3, 10, 14, 16 & 18	Marginal 1, 4, 5, 9, 17 & 19
Soil factors					
Percentage moisture	1981	20.69 ± 0.79	17.05 ± 1.49	5.06 ± 2.05	3.59 ± 1.87
	1983	3.90 ± 1.56	2.55 ± 0.66	3.20 ± 1.38	2.36 ± 0.69
	1984	2.02 ± 0.28	1.82 ± 0.21	1.99 ± 0.20	1.31 ± 0.22
	1985	3.38 ± 2.04	0.83 ± 0.38	1.33 ± 0.21	1.33 ± 0.33
pH	1981	8.21 ± 0.014	8.50 ± 0.091	8.82 ± 0.035	8.94 ± 0.014
	1983	8.84 ± 0.18	9.11 ± 0.093	9.23 ± 0.045	9.13 ± 0.087
	1984	8.67 ± 0.025	8.65 ± 0.018	8.65 ± 0.053	8.62 ± 0.044
	1985	9.44 ± 0.17	9.28 ± 0.060	9.30 ± 0.041	9.34 ± 0.031
Conductivity (μS/cm)	1981	312.0 ± 52.5	213.2 ± 21.7	193.5 ± 19.1	165.8 ± 16.1
	1983	370.0 ± 6.6	289.0 ± 84.6	227.3 ± 29.7	276.7 ± 22.5
	1984	234.7 ± 117.4	216.2 ± 15.6	257.7 ± 45.9	246.2 ± 41.0
	1985	178.0 ± 4.42	210.5 ± 23.5	208.8 ± 26.7	170.2 ± 5.86
Water factors					
Minimum and maximum depth of water table (cm)	1981	11 to 25	19 to 25	39 to 71	45 to 70
	1983	51 to >100	54 to >100	>100	>100
	1984	51 to 95	48 to >100	>100	>100
	1985	66 to >100	84 to >100	>100	>100
pH	1981	7.70 ± 0.13			
	1983	7.33 ± 0.28			
	1984	7.44 ± 0.29			
	1985	*			
Conductivity (μS/cm)	1981	798.3 ± 81.9			
	1983	2950.0 ± 949.9			
	1984	867.0 ± 133.0			
	1985	*			

* Water was too deep to obtain a satisfactory sample.

bution of vegetation, and there was no significant correlation between factors. The isolines that were plotted (Avis, 1983) did not show the same trends observed in 1981 (Fig. 3). Rather than illustrating this graphically, we have divided the sampled quadrats into four regions based on the isolines in Figure 3 and calculated mean values of pH, percentage soil moisture, and conductivity for successive years (Table 3). In the initial study, when the rainfall and soil moisture was high, a noticeable difference between the soil factors of the different regions existed. The very low soil moisture values measured in subsequent years are very similar to those measured on the dunes (Lubke, 1983). The highest values were always recorded in the center of the slack, but the water table was much deeper after 1981 (Table 3).

The pH values are appreciably higher in years subsequent to 1981, and only in 1983 was there any apparent trend of an increasing pH from the center of the slack towards the outside. A similar result was observed with respect to conductivity. Whereas in 1981 there was a notable decrease in conductivity away from the center of the slack, this same trend was only noticeable in 1983. In the subsequent years no appreciable differences were detectable. Van Tooren et al. (1983) recorded extremely high conductivity values (>10,000 μS/cm) on a beach plain in the Netherlands under dry conditions, but in this case the area was occasionally flooded by seawater. We did note a slight increase in conductivity along the seaward side of the slack (up to 500 μS/cm) in the dry period of 1984, when there was a possible accumulation of salts in the sand from salt spray. During a low rainfall cycle one may anticipate a buildup of saline conditions in the dune slack, since there is insufficient rain to flush the salts from the slack system, but this was not observed. In 1983 there was an unexplainable increase in soil water conductivity to almost 3,000 μS/cm, but this appeared to be temporary. The

soil water pH remained constant during this period (Table 3).

DISTRIBUTION OF PLANTS IN THE DUNE FIELD

The distribution of plants across the dune field is best illustrated in the profile program of 1981 (Fig. 5). Changes that occurred on the foredunes were recorded in February 1985 (Fig. 6) and include an increase in the pioneer creeper *Ipomoea brasiliensis* and other indigenous pioneers, as well as the exotic shrub *Acacia cyclops*. This resulted in an increase in species diversity, which is discussed later. The unvegetated foredunes often change in shape and character, but since the pioneer species play an important role in stabilizing sand (Fig. 4), this region has changed very little over the period of the study. The role of *Ammophila arenaria* (marram grass) in foredune stabilization in Europe and North America (Ranwell, 1972; Wiedemann, 1984) and of other species in Australia (Hesp, 1984) is performed by *Scaevola plumieri*, *Sporobolus virginicus*, and *Arctotheca populifolia* along our coastline. These pioneer species are not ubiquitous along the whole coastline due to the severity of the Eastern Cape climate. Young seedlings of these plants have been observed in unvegetated regions of the dune field following periods of high rainfall, usually exceeding 100 mm in a month (Fig. 1), but unless favorable conditions continue they will not become established. Arid conditions prevail for long periods; mobile foredunes, as seen in the background of Figure 4, are thus more common. Vegetative spread of pioneer plants by rhizomes (*Sporobolus virginicus*), stems that can tolerate burying (*Scaevola plumieri*), or stolons (*S. virginicus* and *Ipomoea brasiliensis*) are the most important means of dispersal of these plants during drier periods such as in the 1980s.

Following the moist periods in 1980, the dune slack community was very well developed and supported a wide diversity of species (Lubke, 1983). The extensive area of vegetation at this time is apparent when comparing the photographs of the line transect (Fig. 7). The movement of wind-borne sand to the east has buried much of this vegetation, resulting in the study slack becoming the center of greatest species diversity (Fig. 7D).

Scaevola plumieri plants occasionally become established on the rear dunes (Figs. 5–7) if there is a continuous supply of sand. These plants, like *Ammophila arenaria* (Ranwell, 1972), require mobile sands; salt spray may also be favorable for their growth. A greater supply of salt accumulates in this area than in the dune slacks (Table 2).

There are more herbaceous species close to the coastal scrub in the second profile (Fig. 6). These species, e.g., *Silene primuliflora* and *Heteroptilis suffruticosa*, are commonly found growing along the protected margins of the climax dune scrub community along this coastline (Lubke, unpubl. data).

SUCCESSION WITHIN THE DUNE SLACK

The community maps (Fig. 8) and photographs (Fig. 9) show the changes in abundance and distribution of species in the dune slack over a four-year period. It was fortuitous that this study, which was initiated to show the establishment of *Scirpus nodosus* in the moist slack, has proved useful in a study of succession. The percentage frequency and mean density of the dune slack species from September 1981 to February 1985 are presented in Table 4. We have grouped the 25 species into four categories on the basis of their role in succession. Two of these are common pioneers of dunes and dune slacks; nine are herbaceous annuals or perennials, either pioneers or secondary colonizers of dune slacks; seven are sand dune colonizers, which are rare, absent, or only present on the margins of wet slacks; and six are woody dune scrub species usually only found in dune slacks that are at an advanced stage of succession. *Acacia cyclops* is placed in this category, but it is an extremely aggressive exotic invader that is even found on stable foredunes (Fig. 4B).

Following the moist periods in Spring 1979 (Fig. 1), water accumulated in the triangle-shaped depression, and wind-borne seeds of *Scirpus nodosus* recruited from the neighboring slack germinated. By September 1981 these were recorded as large plants (>30 cm) in the moist center of the study site. Additional recruitment of seedlings occurred following the rainy period of November 1980 (plants recorded as 5–30 cm tall in 1981, Fig. 8). Finally, the greatest number of *S. nodosus* seedlings that were recorded in September 1981 were less than 5 cm tall, having germinated in the autumn and spring periods of 1981. The greatest germination probably occurred in April and May, as many seedlings were observed in July (Lubke & Avis, 1982b). In September up to 240 plants per m^{-2} were recorded, giving a mean density of over 100 plants per m^{-2} for the whole slack. Naturally, all of these plants

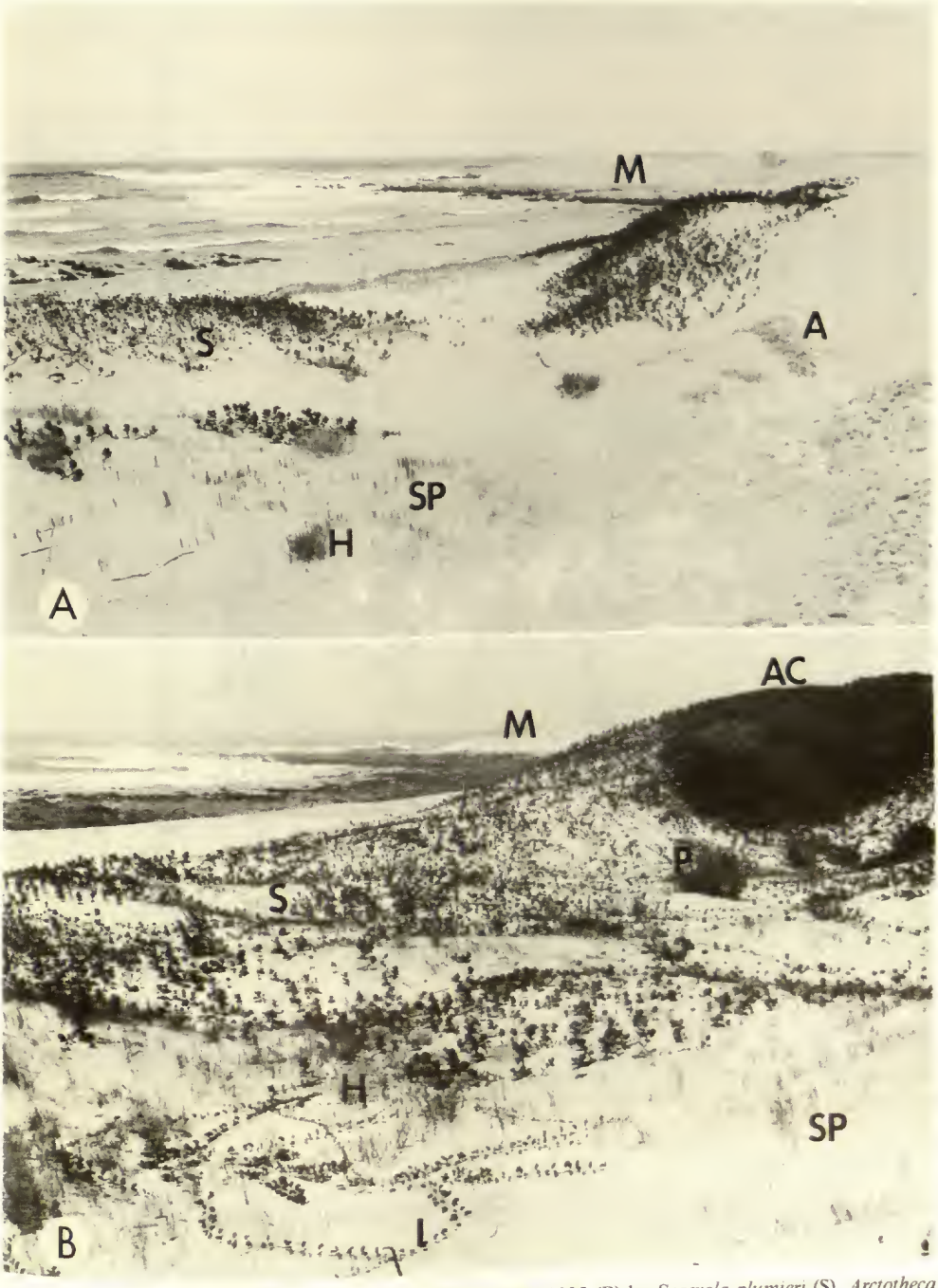

FIGURE 4. Colonization of the foredunes in 1980 (A) and 1985 (B) by *Scaevola plumieri* (S), *Arctotheca populifolia* (A), *Sporobolus virginicus* (SP), *Hebenstretia cordata* (H), *Ipomoea brasiliensis* (I), *Acacia cyclops* (AC), and *Passerina rigida* (P). Mobile dune in the background (M).

FIGURE 5. Profile diagram of the vegetation of the dune field near Klennemonde in July 1981. Species abundance is indicated in the lower part of the diagram as aerial cover in each 1 m² quadrat along the transect.

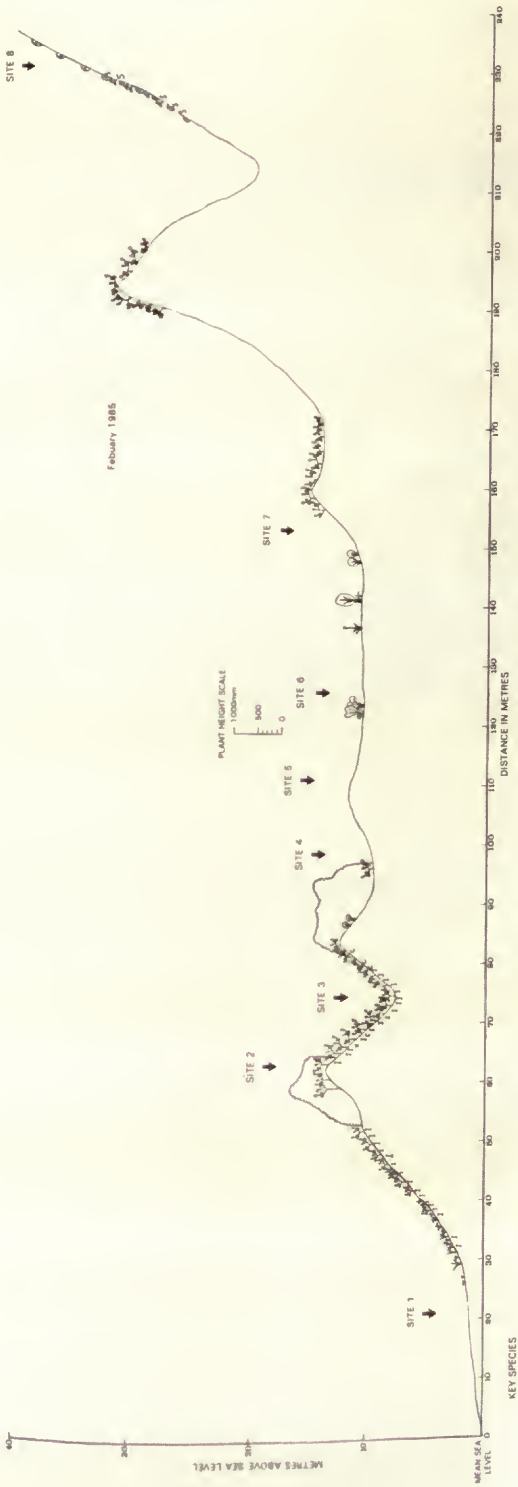

FIGURE 6. Profile diagram of the vegetation of the dune field near Kleinemonde in February 1985. Species abundance is indicated in the lower part of the diagram as aerial cover in each 1 m^2 quadrat along the transect. Sites 1–8 indicate the position of salt traps.

A
B
C
D

FIGURE 8. Map of the vegetation of the dune slack in September 1981, February 1983, January 1984, and February 1985.

could not survive, but because of its favorable start, this sedge has remained one of the dominant species during the years of this study.

There was a very rapid invasion of the dune slack by other species once the pioneers had become established. *Chironia decumbens* and *Vellereophyton vellereum,* which are common in moist slacks of the Eastern Cape (Lubke, unpubl. data), were recorded in the moister areas in September 1981 (Table 4, Fig. 8). The other species present at this period occurred infrequently except for *Sporobolus virginicus,* which may have invaded the wet slack prior to or at the same time as *S. nodosus.* Although common in all slacks and dunes, it favors the drier open habitats, and its frequency and density decreased in the colonized slacks until January 1984, when it was very localized in extent (Fig. 8). By February 1985 it had increased again as fresh sand was deposited in the slack, and we also noted and mapped the spread of the grass along the northern margin of the slack where *Hebenstreitia cordata* also occurred. *Arctotheca populifolia* clumps increased up until 1983 but then died out as the secondary colonizers of the dune slack became more abundant. *Sporobolus virginicus* and *Arctotheca populifolia,* although commonly occurring in dune slacks, do not appear to create the right microenvironmental conditions suitable for the invasion of other slack species, as they are

←

FIGURE 7. The study area and southeasterly direction of the line transect viewed from the rear dune about 200 m from the highwater mark.—A. July 1981.—B. April 1983.—C. August 1983.—D. February 1985. Note how the dune slack vegetation on the right has diminished in size. B and C illustrate the large quantity of sand that was deposited in the slack region from the July 1983 storms.

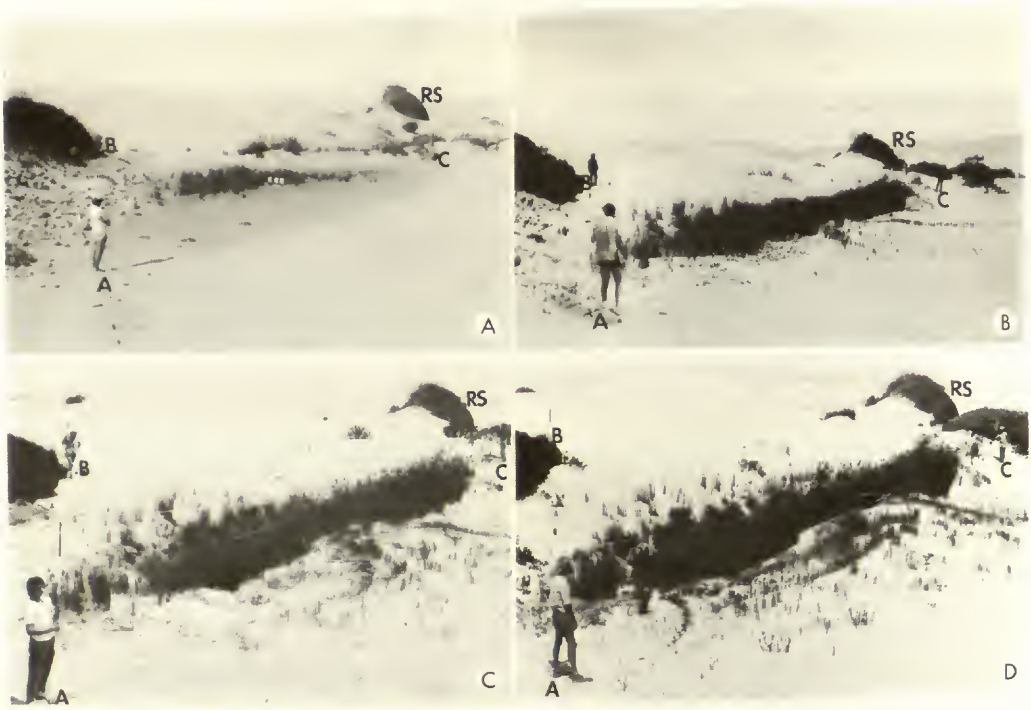

FIGURE 9. Vegetation of the dune slack.—A. September 1981.—B. February 1983.—C. January 1984.—D. February 1985. A, B, and C indicate the margins of the slack. RS = Relic patch of coastal scrub.

often the only species found in the slacks of this region (Lubke, 1983). Moreover, *A. populifolia,* being a true sand dune pioneer, will not co-exist with other species unless a continuous supply of drift sand is available.

Juncus kraussii invaded rapidly from seedlings that germinated in 1982 and 1983, and large plants were recorded in February 1983. By 1984 and 1985 they had outcompeted *Scirpus nodosus* for water and light but were more common along the northern ridge of the dune slack, where dry sand was deposited by easterly winds (Fig. 9C, D). *Scirpus nodosus* and *J. kraussii* occupy similar habitats, yet the latter appears to grow better in the drier slacks. Small *S. nodosus* seedlings (<5 cm) were buried by sand at the western side of the study area due to sand movement by strong westerly winds (Fig. 2) and were not present in 1984 (Fig. 8). This supports our observations that sand movement is important in the establishment of seedlings in the dune environment (Avis & Lubke, 1985).

There has been no marked recruitment of wet dune slack species by seed germination since 1981, due to the lower rainfall during the period of the study (Fig. 1). *Chironia decumbens* grows vegetatively from decumbent stolons and has maintained its presence although the slack has dried out. The Eastern Cape endemic dune slack everlasting *Vellereophyton vellereum* does not grow in dry slacks and was absent after 1983, while the dune everlasting *Helichrysum praecinctum* persists in the drier slack. These composites are annuals, like *Conyza* spp. mentioned below, and possibly have varying germination requirements, *V. vellereum* only germinating under moister habitat conditions. Of the other dune slack colonizers, *Conyza* spp. are weeds of dry areas, *Ficinia lateralis* is common in dry slacks, pebble beaches, and blow-out areas, while *Helichrysum cymosum* is a widespread mesophyte found in many coastal and inland herbaceous communities.

When examining the density of the species as a whole (Table 4), it is notable that in 1981 *Scirpus nodosus,* even excluding the smallest seedlings, had an initial density greater than that of all other species combined (11.7 compared with 10.1 plants m^{-2}). The density of *S. nodosus* plants declined rapidly to 1.6 plants m^{-2} in 1985, while the density of the "other" species increased largely due to the increase in numbers of *Juncus kraussii.* The peak density of the "other" species was 11.5 plants m^{-2} in 1983; then as the slack

TABLE 4. Percentage frequency and mean density of dune slack species in successive years.

	Species	Percentage Frequency				Density (plants m^{-2})—Mean ± Standard Error			
		September 1981	February 1983	January 1984	February 1985	September 1981	February 1983	January 1984	February 1985
Foredune and slack pioneers	1. *Sporobolus virginicus*	40.0	42.8	26.7	46.7	4.9 ± 1.8	3.0 ± 1.3	1.53 ± 0.96	2.73 ± 1.06
	2. *Arctotheca populifolia*	6.7*	14.3	0	–	0.06*	1.22 ± 0.93	0	–
	3. *Scirpus nodosus* <5 cm	60	0	–	–	104.1 ± 37.7	0	–	–
	5–30 cm	40	14.3	0	–	9.6 ± 6.9	0.5 ± 0.37	0	–
	>30 cm	33.3	42.8	53.3	60.0	2.1 ± 1.3	1.79 ± 0.63	2.2 ± 0.81	1.6 ± 0.47
	4. *Juncus krausii*	0	42.8	60.0	53.3	0	2.86 ± 1.32	2.47 ± 0.93	2.33 ± 0.82
	5. *Vellereophyton vellereum*	26.7	35.7	–	–	1.6 ± 1.1	2.14 ± 1.14	–	–
Dune slack colonizers	6. *Chironia decumbens*	13.3	14.3	33.3	33.3	3.06 ± 2.5	1.64 ± 1.43	2.73 ± 1.39	2.33 ± 0.60
	7. *Conyza pinnatifida*	–	0	13.3	6.7*	–	0	2.27 ± 2.13	0.87 ± 0.59
	10. *Helichrysum praecinctum*	33.3	14.3	26.7	20.0	0.8 ± 0.4	2.28 ± 1.51	0.60 ± 0.29	1.4 ± 0.01
	11. *Ficinia lateralis*	–	–	–	6.7*	–	–	–	0.13 ± 0.13
Sand dune colonizers	12. *Scaevola plumieri*	0	0	0	6.7*	0.4*	0	0	0.07 ± 0.07
	13. *Hebenstretia cordata*	6.7*	6.7*	0	13.3	0.6*	0.07*	0	0.67 ± 0.17
	14. *Heteroptilis suffruticosa*	0	0	13.3	0	0	0	0.13 ± 0.09	0
Dune scrub species	22. *Myrica cordifolia*	6.7*	0	6.7*	0	0.4*	0	0.07*	0
	24. *Passerina rigida*	–	21.4	13.3	13.3	–	0.29 ± 0.16	0.27 ± 0.21	0.27 ± 0.21

* Occurred in only one quadrat; 0, present but not recorded in quadrats; –, absent from the dune slack.

TABLE 5. Diversity and dominance of species in the foredunes in 1980 and 1985. (Foredunes are defined as the first 90 m of the transect.)

Index	1980	1985
Simpson's Diversity—Ds	0.642	0.766
Shannon Diversity—H'	0.604	0.700
Simpson's Dominance—ℓ	0.358	0.234

dried out, some species died (e.g., *Vellereophyton vellereum*) or were ousted as shady stable conditions were unsuitable (e.g., *Arctotheca populifolia*), resulting in a decrease in density.

This dune slack is similar in species composition and abundance to the slack of the Alexandria dunefields studied by McLachlan et al. (1987), except for the absence of *Gazania rigens* var. *uniflora* and *Psoralea repens*, which are important slack colonizers in that region. The latter is not found at Kleinemonde and has not been recorded further east than Boknes (Lubke, unpubl. data). Being a Cape species (Bond & Goldblatt, 1984), it is probably at the northeasterly limit of its range.

The migration of an abundance of dune scrub woody plants into the dune slack heralded a third stage in the succession. Initially only *Myrica cordifolia* was present as it invaded vegetatively from the rocky dry southern margin of the study site. As a more diverse community of herbs became established, so more woody dune scrub species germinated from seed carried in by wind or birds. By February 1985, six species were flourishing mainly in the southern region. The exotic *Acacia cyclops* had also invaded from the dunes at point B (Fig. 8). Of the scrub species, *Passerina rigida*, *Metalasia muricata*, and *Stoebe plumosa* are most important, being codominants in the scrub stage of sand dune succession. *Passerina rigida* is the most widespread dominant of this stage in the succession and is the only one of these three scrub species found in the Natal and Zululand coastal dunes (Moll, 1968, 1969; Ward, 1980).

There is no easy explanation as to why and when the invasion of shrubs into the slack dominated by sedges, rushes, and small herbs should occur. Seeds are carried to remote slacks by wind in most cases except for seeds of *Rhus crenata* and *Acacia cyclops*, which are bird dispersed. *Rhus crenata* is a common shrub dominant along the coastal scrub margin (Avis, unpubl. data); and *Myrica cordifolia*, which is possibly dispersed by small mammals, is dominant in bush clumps or pockets within the dune fields (McLachlan et al., 1982) or blow-out areas in the coastal scrub (Lubke, unpubl. data). For scrub seeds to germinate and become established in the slack, the microclimatic factors (namely light, humidity, temperature, and moisture regimes) prevailing within the dense herbaceous community must be suitable. We noted a rapid increase in numbers and diversity of shrub species during the course of 1984, although regular counts were not made. More detailed autecological studies of these plants are required to explain the factors governing their establishment in the dune slacks. The absence of high rainfall during this period indicates that the moisture conditions of the slack were not adverse to shrub seed germination and seedling establishment.

Present indications (Figs. 8, 9; Table 4) are that under the right environmental conditions of higher rainfall and lower winds, the shrub species may replace the herbaceous species in the region of our initial study site and that the pioneers will move to the north and east. Thus there appears to be an overall northeasterly migration of the slack vegetation as existing plants are buried by sand moving across from the west, an observation that was also made by McLachlan et al. (1987) in the Alexandria dune slacks.

CHANGES IN DIVERSITY AND DOMINANCE

Diversity and dominance indices were calculated for the foredunes using the cover index of each species in each linear meter along the first 90 m of the transects (Figs. 5, 6) as the measure of abundance. There was a slight change in dominance (Table 5) over the five-year period, as other species apart from *Scaevola plumieri* and *Sporobolus virginicus* became more frequent on the foredunes in 1985. These foredunes are atypical for the Eastern Cape coast, since more often a single pioneer is found colonizing the mobile sands resulting in stable hummocks (Lubke, unpubl. records). Species such as *Gazania rigens* var. *uniflora*, *Tetragonia decumbens* (which were not recorded here), or *Arctotheca populifolia* are common locally in many areas along this coastline. There is also a change in diversity from 1980 to 1985, as indicated by both diversity indices (Table 5). The increase in diversity is noticeable on the profile diagrams (Figs. 5, 6). Younger adjacent foredunes are colonized more exclusively by *Scaevola plumieri*, and it would appear that this species was the original dominant pioneer of the dunes and that the other species are invading in the process of succession.

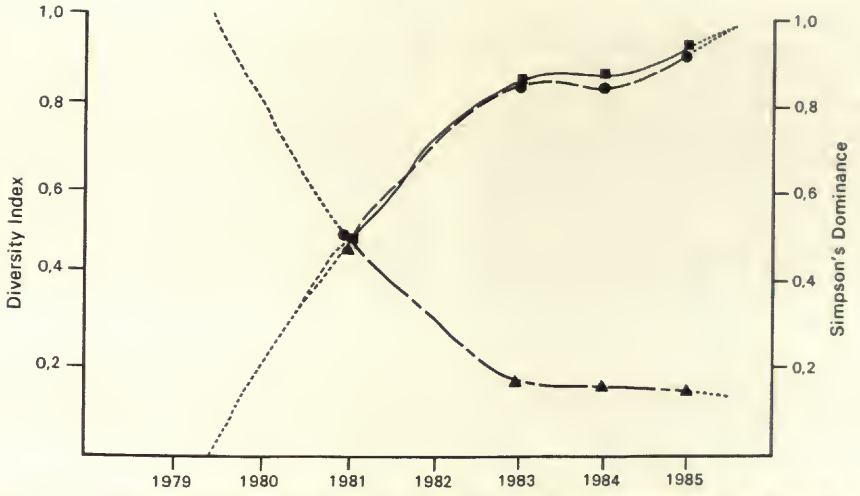

FIGURE 10. Changes in diversity and dominance of the species in the dune slack over a six-year period. ■—■ Shannon index (H'), ●- - -● Simpson's index (Ds), and ▲—— —▲ Simpson's dominance (ℓ).

Passerina rigida, a notable dominant of the dune scrub stage (Moll, 1969), is also present on the foredune (Fig. 4B).

The diversity and dominance indices for the dune slack site were calculated using the density data of all species in the measured quadrats. These results are plotted in Figure 10. There was an initial rapid increase in diversity as new species invaded the slack, with little observable differences in the values obtained for the two indices. Dotted lines were extrapolated back to 1979 (Fig. 10), when it is assumed that *Scirpus nodosus* was the sole colonizer of the slack and, hence, diversity would have been zero. After 1983 the diversity increased more slowly as other species invaded the slack. After reaching a maximum diversity one would expect a drop in diversity in the climax dune scrub community as one or more shrubs become dominant. There was a corresponding decline in dominance starting from the point when *Scirpus nodosus* was the only species, but the dominance index will probably increase with time as a climax dune scrub community is attained.

Discussion

Ideally, a study of succession requires long-term observations, a record of environmental variables during the period of study, and experimental evidence to substantiate the findings. Although our study period of five years is not very long, in conjunction with the experimental and environmental data, we are able to draw conclusions about the dynamics of the sand dune and slack vegetation (Fig. 13). Of the other studies on coastal dune vegetation in South Africa, Moll (1969) and Ward (1980) discussed successional changes along the Natal coast, but their findings were not substantiated by experimentation or long-term data records. Pammenter (1983) and Donnelly & Pammenter (1983) have made detailed ecophysiological studies of dune species, and McLachlan et al. (1982, 1987) studied the total dune slack ecosystem and drew some conclusions about succession.

Weisser (1978a, 1978b) and Weisser & Marques (1979) used air photo interpretation to show gross vegetation changes in the dune areas near Richards Bay between 1937 and 1974. In this more tropical region with a hot, humid climate and a mean annual rainfall of over 1,200 mm, successional changes are fairly rapid. By contrast, Lubke (1983) studied air photos of the Kleinemonde area for the same period and was unable to detect marked vegetational changes. Thus climate is undoubtedly the major limiting factor in dune succession. However, this technique has proven useful in the Eastern Cape in an area where exotic species were used for foredune stabilization. Rapid changes occurred in the dune fynbos as succession was speeded up in the protected slack and rear dune environment (Lubke, in prep.).

The dune slack region of the dune fields is the critical zone of colonization and stabilization. Even if the foredunes have been stabilized by pioneer vegetation, it is only after a mature dune

1981
1983
1984
1985
LEGEND
Dune and Slack Pioneers
1 Sporobolus virginicus
2 Arctotheca populifolia
Dune Slack Colonizers
3 Scirpus nodosus
4 Juncus krausii
5 Vellereophyton vellereum
6 Chrysanthemoides monilifera
7 Conyza bonariensis
8 Conyza scabrida
9 Helichrysum cymosum
10 Helichrysum praecinctum
11 Ferraria lateralis
Sand Dune Colonizers
12 Scaevola plumieri
13 Hebenstretia cordata
14 Heteropsis auriculata
15 Ipomoea brasiliensis
16 Silene primuliflora
17 Zaluzianskya maritima
18 Senecio elegans
Dune Scrub Species
19 Stoebe plumosa
20 Athanasia trifurcata
21 Metalasia muricata
22 Myrica conifolia
23 Rhus crenata
24 Passerina rigida
25 Acacia cyclops

slack community is produced that the climax dune scrub or dune forest vegetation may develop. We have not observed the complete process of succession in the last five years, but our observations on the dune slack together with experimental evidence have led to an understanding of succession on the whole dune system.

Following the wet period of 1979 (Table 1; Fig. 1), the slack was colonized by *Scirpus nodosus* (species number 3) in 1979 and 1982. The changes in relative density of all species are summarized in the form of pie charts (Fig. 11) that show that this pioneer sedge was most abundant in September 1981. Moving in a clockwise direction, the arrows illustrate species replacement under wet conditions. *Juncus kraussii* (4) became increasingly important. A much greater diversity of species was recorded from 1983 to 1985, and the dominance of *Scirpus nodosus* (3) decreased (Figs. 10, 11). Since it favors wet slacks, *Vellereophyton vellereum* (5) disappeared during the dry period, when the soils dried out, the water table dropped (Table 3), dry sand was blown into the slack by strong winds (Figs. 2, 7), and rainfall decreased (Table 1; Fig. 1).

The counterclockwise arrows on the pie charts (Fig. 11) illustrate the successional replacement of species in dry regions of the slack moving towards the more advanced stages of succession. The widespread grass *Sporobolus virginicus* (1) is always abundant, and sand dune colonizers (12–18) increased in abundance during the course of this study as dry conditions prevailed. Succession from both dry (counterclockwise arrows) and wet (clockwise arrows) slack conditions results in the dune scrub stage. *Passerina rigida* (24), an invader of drier areas, was most common, but five other species (19–23) were also recorded in 1985. These young shrubs are evident in the photograph of the slack taken in February 1985 (Fig. 9D). Should favorable conditions continue, these species will become more abundant as was observed in the older slack community of 1980 (Figs. 5, 7). There is evidence of a much more widespread and extensive coastal scrub vegetation in these dune fields as relic patches of coastal scrub occur within the drift sands (see background of the photographs, Fig. 9) and the coastal scrub is probably contracting (Fig. 12).

Seed dispersal and the establishment of seedlings within the dune and slack environment are the most critical stages of succession. Studies in the Gulf of Mexico by Altamirano & Guevara (1982) and Castillo & Carabias (1982) on phenology and seed distribution of dune species respectively have shown that seed production is prolific and a mean density of 629 seeds m^{-2} is common in dune fields. Records on coastal species of the Eastern Cape (Lubke, 1988) indicate that our dune species also flower and produce seeds throughout much of the year, and the availability of seed in all habitats is unlikely to be limiting.

Models of seed germination and seedling establishment in the dune environment have been produced by van der Valk (1974) and Guevara (1982) for the North Carolina and the Mexican Gulf coasts respectively. While they note the importance of many factors, shifting sand appears to be the most vital in determining the successful establishment of young plants. We observed the germination of species on the foredunes and in the slacks during the course of this study following periods of high rainfall (Fig. 1), and these seedlings were used in experimental studies (Avis, 1983). Whereas Buckley (1982) found soil catena were major factors in the success of transplants on sand ridges in central Australia, our studies (Avis & Lubke, 1985), like those of van der Valk (1974), showed that sand movement due to high winds (Fig. 2A) caused burial and subsequent death of the seedlings. Even in regions out of the normal range of *Scirpus nodosus*, where sand movement was minimal (next to the coastal scrub, at site 8 in Fig. 5), survival of the transplanted seedlings was more successful.

On the foredunes, *Scaevola plumieri*, *Ipomoea brasiliensis*, and *Arctotheca populifolia* seedlings are commonly found during cooler moist periods (Fig. 1). There is less likelihood of erosion or burial of the seedlings when the sand is moist. Seeds of *Sporobolus virginicus* are difficult to germinate (Breen et al., 1977), and the vegetative spread of mature plants is the common method of dispersal of this species. Once pioneer plants have become established (Fig. 13), they play an important role in sand stabilization and dune building (Hesp, 1983, 1984). *Scaevola plumieri*

FIGURE 11. The changes in relative density of all the species of the dune slack over the period September 1981 to February 1985. Clockwise arrows represent successional replacement of species from wet slack to dune scrub and counterclockwise arrows illustrate replacement of species from dry slacks or dunes to dune scrub.

FIGURE 12. The study slack photographed in January 1984 with the direction of the line transect illustrated. The arrow indicates the retracting coastal scrub at the top of the rear dune.

produces woody stems that ramify and branch as sand is deposited, resulting in large extensive foredunes parallel to the coast (Pammenter, 1983). This species is widespread along tropical (Morton, 1957) and subtropical coasts of Africa (Moll, 1969; Ward, 1980). *Sporobolus virginicus,* a cosmopolitan grass with shallow underground rhizomes and surface stolons, stabilizes dunes in a similar way (Henriques et al., 1984; Gooding, 1947), but it is also found in the dune slack and is probably not dependent on a continuous supply of sand and salt spray as is *S. plumieri* (Pammenter, 1983). The tufted composite species, *Arctotheca populifolia* and *Gazania rigens* var. *uniflora,* and procumbent *Tetragonia decumbens* form small hummock dunes that are not easily invaded by other dune-colonizing species. Moreover, these hummocks are often unstable (Wiedemann, 1984). The other dune-colonizing species, e.g., *Hebenstretia cordata,* penetrated into the *Scaevola* zone (Figs. 4–6), resulting in an observable change in species diversity and dominance over the five-year period (Table 5). *Ipomoea brasiliensis* is also cosmopolitan and produces distinct vegetation zones behind the pioneer zone in Barbados (Gooding, 1947). Van Tooren et al. (1983) found that life form is important in succession, but our dune species do not conform to any life form–habitat pattern, as each stage is composed of a variety of life forms.

Salt spray may be a limiting factor on the foredunes, since it affects the growth of seedlings (van der Valk, 1974; Lubke & Avis, 1982b). However, the foredune species are more resistant to salt spray, and it has proven difficult to correlate salt spray with vegetation zonation (Donnelly & Pammenter, 1983). Van der Valk (1974) found that salt spray played a secondary role to sand movement in eliminating forbs from the foredunes. However, salt spray is also important in the supply of nutrients to the sand, but rapid leaching of nutrients by rain results in a low cation exchange capacity of dune sands (van der Valk, 1974). This tends to limit the growth of species on dunes (Willis, 1963; Willis & Yemm, 1961; Onyekwelu, 1972). There must therefore be a balance between nutrient supply from salt spray and the ability of the foredune species to withstand salt damage.

Although moisture is unlikely to be a factor

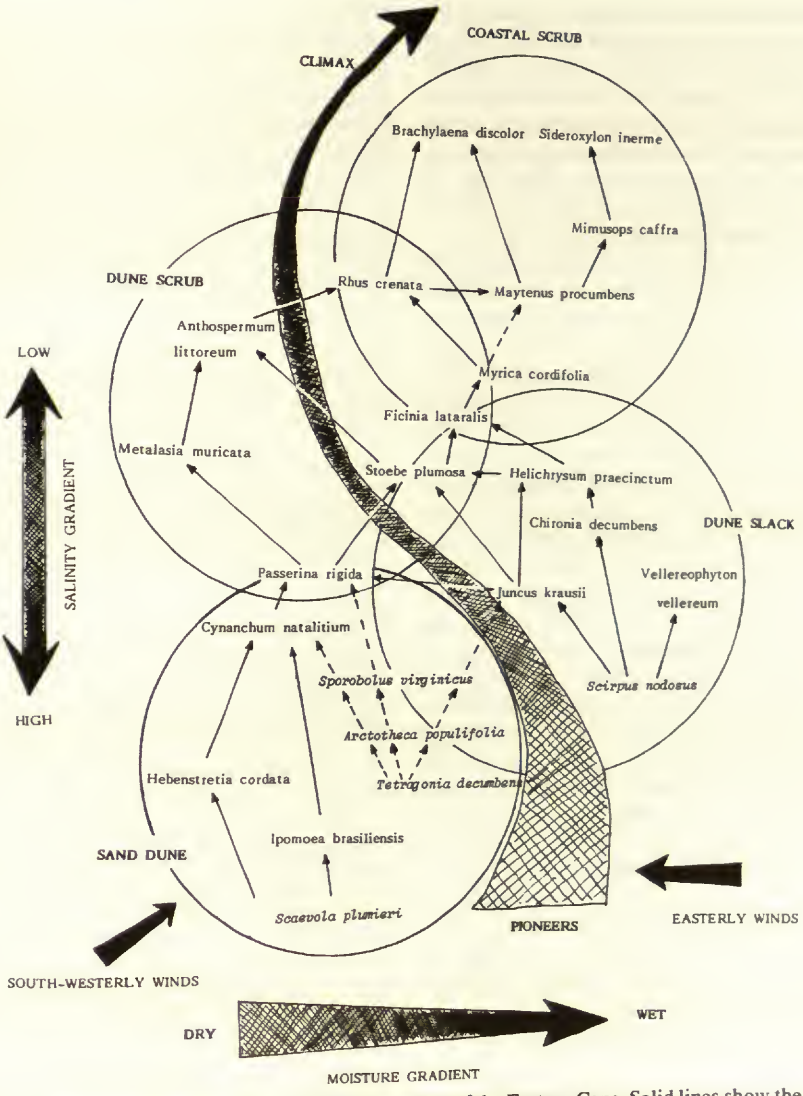

FIGURE 13. A model of plant succession in the dune fields of the Eastern Cape. Solid lines show the common and dashed lines the less common successional pathways. Not all species found at Kleinemonde are included in the diagram, and additional species not found in the study area are added for completeness of the successional model.

limiting the growth of mature plants such as *Scaevola plumieri* on the foredunes (van der Valk, 1974; Pammenter, 1983), we have found it to be of much greater consequence in the dune slacks. The loss of species (e.g., *Vellereophyton vellereum*) in our study area during a dry cycle (Table 4; Fig. 1) has been noted as a periodicity of species fluctuation in the beach plain of the Netherlands by van Tooren et al. (1983), whose study extended over a longer (10-year) period. We can thus predict that with the return of wetter conditions, these slack species will reappear, since the wet periods are important in the establishment of a more diverse slack flora. With higher soil moisture (Fig. 3) successful seedling establishment of *Scirpus nodosus* was achieved (Figs. 8, 9), and under these conditions the diversity (Fig. 10) and abundance of other species (Fig. 11) increased. In contrast, during drier periods and in drier regions of the slack, for example to the

north of the study slack (Fig. 8), *Sporobolus virginicus* and *Arctotheca populifolia* may colonize the sands but the diversity of species will not increase. In our model (Fig. 13) we therefore show that the greatest diversity of slack species is most likely to occur when *Scirpus nodosus* is the pioneer of a wet slack (clockwise arrow, Fig. 11) and not via dry slacks colonized by the latter two species (counterclockwise arrow).

Other soil factors such as conductivity and pH (Table 3; Fig. 3) do not appear to be correlated with vegetational development. However, the buildup of nutrients as a result of humus decomposition (van der Valk, 1974; Guevara, 1982) must be an important factor in the successful invasion and establishment of other species in the dune slack. Nutrient levels have not been measured in this area, and studies of this nature would be important in substantiating this conclusion. Air temperatures and consequently soil temperatures vary according to the site and aspect (Oosting & Billings, 1942). They are lower or less extreme in the slacks (Lubke, 1983), and since seedling establishment occurs during the cooler periods, it is not a factor that is likely to be of paramount importance in pioneer vegetation establishment, either on the dunes or in the slacks. However, once the *Scirpus–Juncus* stage in the slack or the *Scaevola* stage on the dunes is achieved, a favorable microclimate has been created for seeds of other species to germinate and young plants to become established.

Of the dune scrub woody plants, *Passerina rigida* is the first to invade the dunes (Figs. 5, 6) and the dune slacks (Figs. 8, 11), as it can tolerate a variety of soil moisture and sand movement regimes. Other shrub species rapidly invade, and the study slack has achieved the dune scrub stage in our model (Fig. 13). It will require a few years for these shrubs to mature and become successful colonizers of the dune slack. *Rhus crenata* links our observed succession (Fig. 11) to the successional model (Fig. 13), as it is a common dominant along the margins of the coastal scrub (Lubke & Avis, unpubl. data). The climax trees of this coastal scrub or thicket (Lubke, 1988) are the milkwoods *Sideroxylon inerme* and *Mimusops cafra,* and *Brachylaena discolor,* depending on locality and prevailing conditions. *Myrica cordifolia* is common on pebble beaches and in blow-out areas of the coastal scrub and has been recorded as dominant in bush pockets (McLachlan et al., 1982) in the Alexandria dune fields. The accumulation of humus and the development of a soil profile is important in the succession of large woody shrubs and trees on drift sands (Moll, 1969). Lubke (1983) recorded a lowering of pH and an increase in conductivity related to a buildup of organic matter in the soils of rocky promontories where climax coastal scrub occurs. The physical effect of wind and salt spray are important additional factors throughout the dune environment and may be a cause of shrub and tree pruning on the rear dunes (Parsons & Gill, 1968; Moll, 1969).

Once vegetation has become established on the foredunes, it does not mean that succession will continue in the direction indicated on our model (Fig. 13). In some areas foredunes may be colonized with extensive unvegetated dune fields between the shore and the climax coastal scrub (Lubke, 1983; McLachlan et al., 1987). The critical stage is thus for dune slacks to become colonized and stable. Under the present rainfall conditions it is unlikely that the dune fields of Alexandria or at Kleinemonde will be naturally stabilized. Should the rainfall become more consistent and exceed 1,000 mm per annum, succession will be speeded up, resulting in rapid vegetational changes similar to those observed near Richards Bay (Weisser, 1978a, 1978b). With an erratic cycle of wet and dry periods (Table 1; Fig. 1) and rainfall never exceeding 600 mm per annum, slack vegetation will never develop much further than the stages observed at present. The occurrence of isolated scrub remnants (Fig. 9) and a retreating coastal scrub margin (Fig. 12) are evidence of a moister, more equitable climate in prehistoric times.

The controlling environmental factor thus appears to be rainfall and soil moisture, for only under moist conditions will a more diverse slack community develop. However, the strong winds (Fig. 2) of this area are the major factor reducing growth of the slack vegetation. Under dry, windy conditions sand movement is sufficient to cause burial of seedlings; adult plants and ultimately the whole slack community disappears. The diminishing size of the slack at Kleinemonde (Fig. 7C, D) is due to these causes, and similar observations have been made along the whole of this coastline during the prevailing dry cycle. When moister conditions return, the slack communities will increase in size but will never attain the climax situation illustrated in our model (Fig. 13), except in a few localized or protected areas.

Conclusion

The major factor controlling the establishment and growth of plants on the mobile dunes is the climate. Under high rainfall and cool conditions, seedlings become established on the foredunes and dune slacks. Even if the foredunes are well colonized, it is only when the slacks become stabilized that succession will proceed to the climax coastal scrub or forest. Under the present dry rainfall regime, the coastal slacks are contracting as dry sands are highly mobile and the prevailing winds predominantly from the southwest deposit large amounts of sand on the existing plant communities. When higher rainfall conditions return, a more diverse slack flora should develop, resulting in an expansion of the vegetation in these regions. Salt spray and soil factors appear to be secondary in the complete successional scheme, but locally or periodically these may be decisive factors in determining the successional pathway. There is evidence that the coastal scrub vegetation has been contracting over a long period of time (hundreds of years). Unless the rainfall increases to over 1,000 mm per annum, it is unlikely that the present dune fields in the Eastern Cape will ever be fully colonized and a climax vegetation attained.

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LATEX TRITERPENOID PROFILES OF NORMAL AND CRISTATA TAXA OF *EUPHORBIA* AND THEIR APPLICATION AS CHEMOTAXONOMIC CHARACTERS

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ABSTRACT

Triterpenoid profiles from laticifer contents of both normal and cristata *Euphorbia* taxa were compared to determine the effects of the abnormal cristata condition upon the stability of the triterpenoid composition in latex. The cause of the cristata condition is unknown but interpreted to be of pathological origin. Taxa of succulent *Euphorbia* examined included *E. lactea* Haw., *E. ledienii* Bgr., *E. mauritanica* L., *E. nivulia* Ham., *E. obesa* Hook. f., and *E. susannae* Marl. Acetone extracts of latex from the shoot apex of each normal plant yielded a distinctive triterpenoid profile for each taxon as determined by gas-liquid chromatography. Latex extracts from the growth apex of cristata plants possessed triterpenoid profiles identical to the normal plant for each taxon. The profile was unaffected by geographical origin. Similarly, analyses of latex from normal and abnormal regions of the same plant possessed identical profiles. The combinations of triterpenoids between the different taxa included in aggregate approximately 15 compounds as indicated by different retention times. Data from this study support an interpretation that the latex triterpenoid profile is stable and unaffected by factors resulting in the induction of the abnormal cristata condition. The stability of these laticiferous compounds in taxa of diverse morphologic-physiological condition and geographical origins is indicative that triterpenoid profiles may provide an additional and important taxonomic character for studies of *Euphorbia*.

RÉSUMÉ

Des profils triterpinoïdes de contenus de laticifères des taxons d'*Euphorbia* à la fois normaux et cristates ont été comparés afin de déterminer les effets de la condition anormale cristate sur la stabilité de la composition triterpenoïde dans le latex. La cause de cette condition est inconnue mais on l'interprete comme étant d'origine pathologique. Les taxons d'*Euphorbia* examinés comprennent *E. lactea* Haw., *E. lendienii* Bgr., *E. mauritanica* L., *E. nivulia* Ham., *E. obesa* Hook. f., et *E. sussannae* Marl. Des études chromatographiques d'extraits d'acétone de latex pris sur le bout de la tige de chaque plante normale ont donné un profil triterpenoïde distinctif pour chaque taxon. Des extraits semblables pour les plantes cristates ont des profils triterpenoïdes identiques à ceux de la plante normale de chaque taxon. Le profil n'est pas affecté par l'origine géographique d'une plante. De même, des analyses de latex des parties normales et anormales de la même plante possedent des profils identiques. Les temps de rétention indiquent qu'environ 15 triterpenoïdes existent parmi les différents taxons. Des données de cette étude portent à croire que le profil triterpenoïde du latex est stable et n'est pas affecté par des facteurs à l'origine de l'induction de la condition cristate anormale. La stabilité de ces produits laticifères dans des taxons de conditions morphologico-physiologique différentes et d'origines géographiques diverses indique que les profils triterpenoïdes peuvent fournir une caractéristique taxoinomique importante de plus pour les études du genre *Euphorbia*.

The normal shoot morphology of succulent *Euphorbia* species may become grotesquely modified in that a shoot apex becomes changed into a growing strip. The altered morphology imparts an irregular fanlike appearance to the apex of plants that are termed cristata varieties (Lamb & Lamb, 1971). While the origin of the cristata condition is unclear, it is interpreted as an infectious condition, a view supported by the occurrence of this phenomenon on succulents in other families (Lamb & Lamb, 1971). The altered morphogenesis is disruptive to several morphological features of the shoot including the development of a strip meristem, modification of stem morphology into a flattened fan-shaped axis unlike a typical stem, reduction in leaf size, reduction in size of leaf-related structures as stipules, and inhibition of flower development. The cristata syndrome as viewed morphologically is undoubtedly accompanied by anatomical and physiological changes less evident, although these associated conditions have not yet been investigated.

The cristata syndrome can alter plant morphology sufficiently to obscure recognition of the taxonomic relationship between the cristata and

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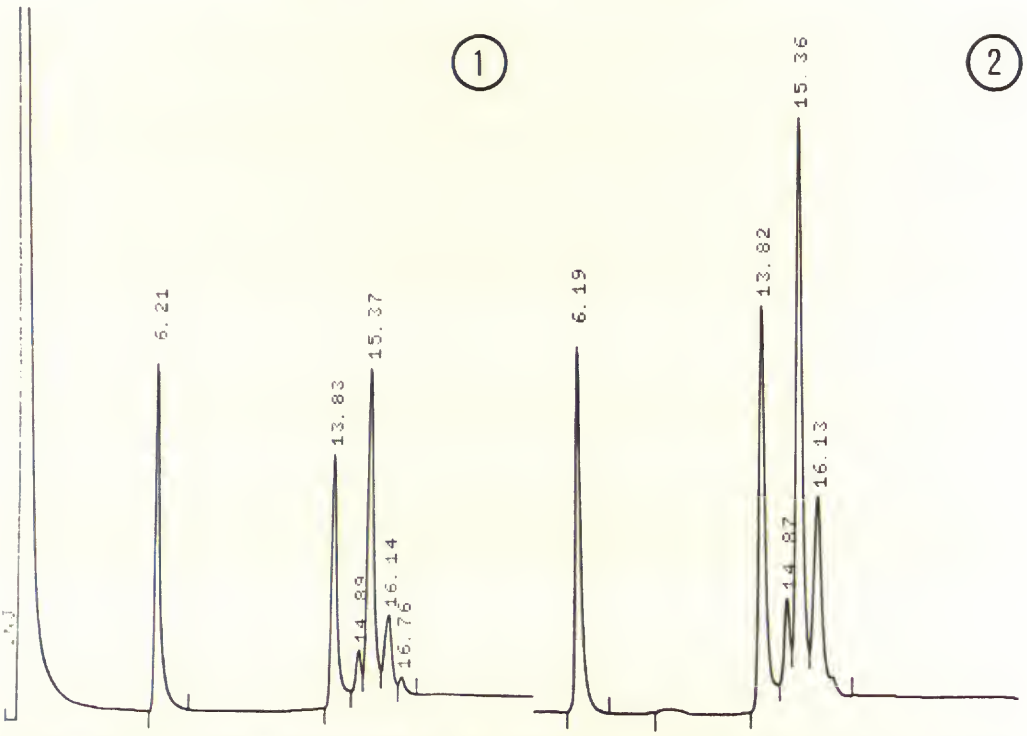


FIGURES 1, 2.—1. Triterpenoid profile of normal *Euphorbia lactea* showing distinctive major peaks and a small peak at RT 16.76. RT 6.21 is IS.—2. Profile of *E. lactea* cristata showing the same profile of peaks as in the normal plant. The shoulder to the right of RT 16.13 represents the small peak RT 16.76 in the normal plant. RT 6.19 is IS.

the normal plant. It is of particular interest, therefore, to determine whether this abnormality extends to biosynthetic activities within the plant because secondary products from *Euphorbia* represent characters of taxonomic value (Mahlberg et al., 1983; Mahlberg & Pleszczynska, 1983). The ready availability of latex from the nonarticulated laticifer of both plant forms for comparative chromatographic analyses makes it possible to evaluate the effect of the cristata syndrome on secondary products synthesized in the squalene pathway by this cell type.

The purpose of this study is to compare the triterpenoid profile in the laticifer from normal and cristata plants and determine whether physiological changes in triterpenoid synthesis accompany the morphogenetic alterations. These analyses will provide a basis for interpreting the level of stability of triterpenoid biosynthesis in the laticifer of both plant forms and assist in verifying the relationship between such forms.

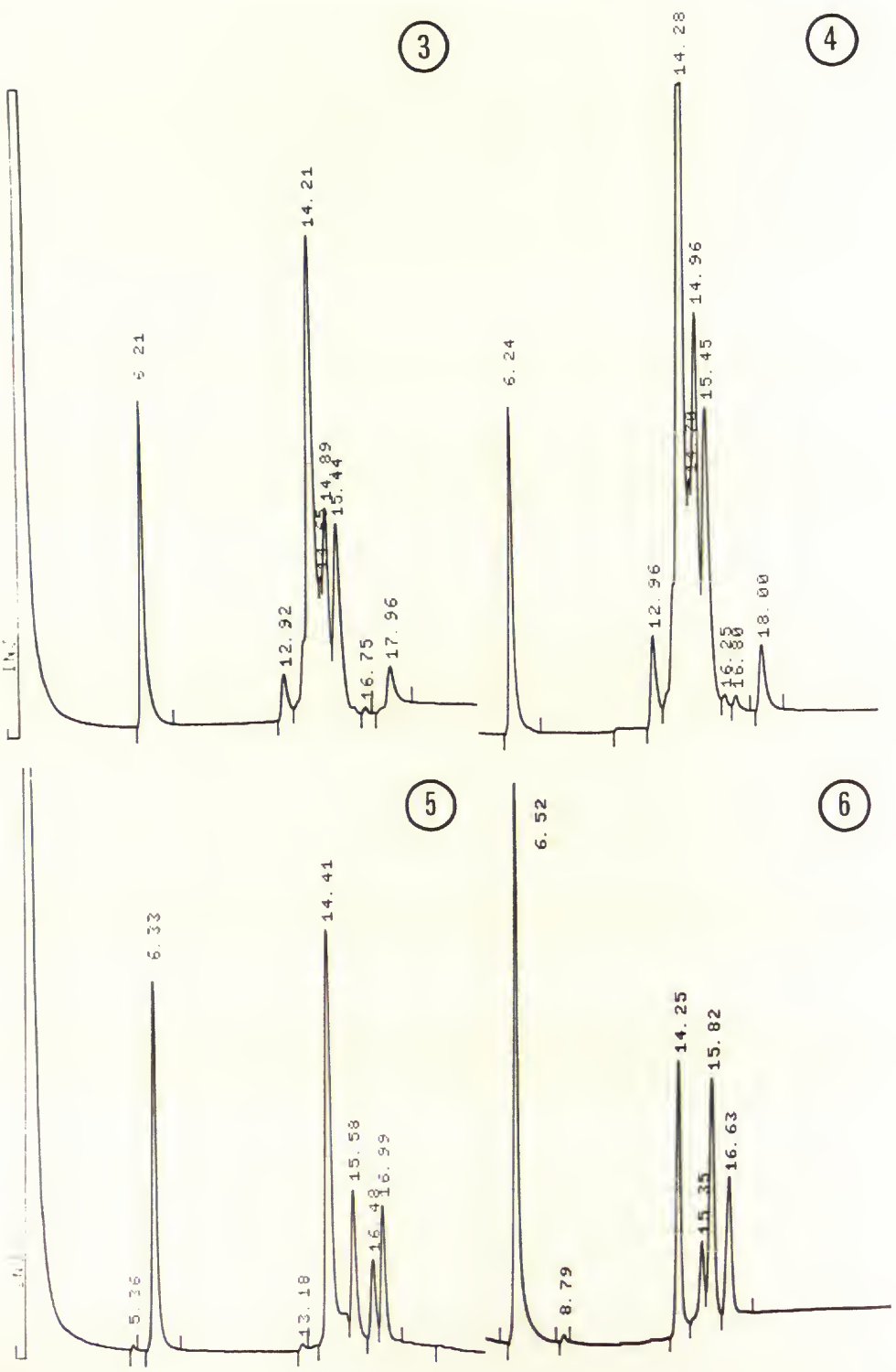
MATERIALS AND METHODS

Living specimens of both normal and cristata plants in the Botanical Garden at the University of Heidelberg are represented by *Euphorbia lactea* Haw. cristata 19620, *E. ledienii* Berger 8982, *E. ledienii* Berger cristata 8956, *E. mauritanica* L. 47028, *E. mauritanica* L. cristata 47028, *E. nivulia* Ham. 95931, *E. obesa* Hook. f. 7599, *E. obesa* Hook. f. cristata 7599, *E. susannae* Marl. 45790, 9257, *E. susannae* Marl. cristata 9257. Specimens grown at Indiana University include *E. lactea* Haw. 11, *E. lactea* Haw. cristata 11, *E. mauritanica* L. 26, *E. nivula* Ham. cristata 104, *E. obesa* Hook. f. 29. Latex was obtained from the apex region by incising the axis in the normal plant and incising directly into the abnormal portion of the axis in the cristata form. The exudate was run into a vial containing 1–2 ml spectroanalytical grade acetone. The acetone supernatant containing the triterpenoids was decanted into a fresh acetone-washed vial and evaporated to dry-

TABLE 1. Percentage composition of triterpenoid components in acetone extracts of latex from normal and cristata *Euphorbia* taxa. s = shoulder, t = trace.

Sample	Retention Time, min.[1]															
	12.12	12.57	12.80	13.13	13.34	13.68	14.11	14.34	14.56	14.78	15.12	15.31	16.04	16.12	16.71	16.87	17.85
E. lactea, normal						30.9				8.1		43.7	14.6		2.7		
E. lactea, cristata						28.9				7.9		42.8	20.4		t		
E. ledienii, normal						57.9		7.3			32.3			2.1		0.4	
E. ledienii, cristata						57.8		7.0			32.4			2.2		0.6	
E. mauritanica, shoot going to cristata	9.4	9.6		4.6		t	14.7			21.4		20.5		17.7	2.1		
E. mauritanica, cristata	4.9	6.3		3.3		1.6	16.2			26.2		20.2		17.5	2.9		
E. mauritanica, normal shoot on cristata	6.5	6.4		3.4		0.4	16.1			23.7		21.2		19.2	3.1		
E. nivulia, normal		0.2				31.6				13.0		32.2	22.1		0.9	—	
E. nivulia, cristata		—				25.2				17.1		30.1	26.8		—	0.8	
E. obesa, normal			3.3				47.2	s	4.5	16.5		19.1		1.7	2.6		5.1
E. obesa, cristata			3.9				49.8	s	4.7	19.2		17.4		1.0	0.9		3.1
E. susannae, normal			1.2		0.8		54.9	s				19.9		8.1	15.1		
E. susannae, cristata			—		—		63.1	s				14.7		6.6	15.6		

[1] Retention times corrected to IS 6.50 and presented as a mean for all samples.


3
6.21
12.92
14.21
14.89
15.44
16.75
17.96
4
6.24
12.96
14.28
14.96
15.45
16.25
16.80
18.00
5
5.36
6.33
13.18
14.41
15.58
16.48
16.99
6
6.52
8.79
14.25
15.35
15.82
16.63

ness over nitrogen. Each sample was prepared for gas-liquid chromatography as described elsewhere (Mahlberg & Pleszczynska, 1983; Mahlberg et al., 1983). Androstenedione (Δ^4-androsten-3,17-dione) was used as the internal standard (IS). Individual compounds were quantified on a Hewlett-Packard 3380A integrator with data on detected peaks expressed as area percent. Individual retention times (RT) were compared with RT values of known standards for preliminary determination of specific compounds in the samples. The tabulated RT values for all analyses were corrected by calculation to a uniform RT 6.50 min. to facilitate direct comparisons of all chromatograms. Therefore, the RT values on original chromatograms shown as text figures differ somewhat from calculated RT values in the table. Quantitative data on peak pairs and between peaks were compared statistically to evaluate the differences between peak ratios composing the profiles of normal and cristata forms for each taxon. The term triterpenoids is used here to include both sterols and triterpenes.

Results

Latex extracts from each of the examined normal plants show a characteristic triterpenoid profile for each taxon as exemplified by *Euphorbia lactea* (Fig. 1) and *E. obesa* (Fig. 3). Although several compounds are common between the normal plants, the taxa contain both qualitative and quantitative differences for the triterpenoids (Table 1). The same chromatographic program was employed for analyses of all samples to facilitate direct comparison of the profiles from the different taxa as shown in all figures. The profile is represented by the prominent triterpenoid components with RT values ranging from approximately 12–18 min. In addition to these major peaks, small quantities of other triterpenoids may be present but obscured by other compounds. For example, the two shoulders at the left of peak RT 14.28 for *E. obesa* (Fig. 3) represent unrecorded components. Other components are represented by trace amounts and identified at levels under 1% of the total composition (Table 1).

A comparative analysis of latex from normal and cristata plant-pairs for a taxon show both samples to possess comparable triterpenoid profiles (Figs. 1–4). Although the abnormal forms show the typical cristata syndrome, their triterpenoid profile remains comparable to the normal plant. In comparisons of two-sample groups in each plant pair, both members contain the same peaks and approximately the same percentage of each compound (Table 1). These results are evident for plant pairs possessing a small number of peaks as in *Euphorbia nivulia* (Fig. 6) or in pairs possessing a more complex pattern of triterpenoid peaks, as in *E. obesa* (Figs. 3, 4). In a two-sample group from normal and cristata *E. lactea* the percentages of the compounds represented as the several peaks include 30.9 and 28.9 (RT 13.68), 8.1 and 7.9 (RT 14.78), 43.7 and 42.8 (RT 15.31), 14.6 and 20.4 (RT 16.04), and 2.7 and a trace (RT 16.71), respectively. Similar comparisons for each of the taxa are presented in Table 1.

Stability of the profile for a taxon is retained in normal and cristata forms of diverse origins. For plant pairs derived from a common clone, as exemplified in *Euphorbia lactea, E. mauritanica, E. obesa,* and *E. susannae,* the triterpenoid profiles are identical in both forms (Figs. 1–4; Table 1). The continuity of triterpenoid composition also is apparent in reverted tissues, as in the cristata forms of *E. lactea* and *E. mauritanica,* in which new normal shoots derived from axillary buds on the cristata plant are found to possess the characteristic triterpenoid composition of the normal parental stock (Table 1).

Extracts of normal and cristata plants of different clonal origins and maintained at different geographical locations also show stability for the triterpenoid profile. Paired *Euphorbia lactea* specimens grown over 20 years at Indiana University show matched profiles for paired specimens of *E. lactea* grown at Heidelberg University (Fig. 1). Similarly, normal and cristata forms of *E. susannae* and *E. nivulia,* although derived from

←

FIGURES 3–6.—3. Triterpenoid profile of normal *Euphorbia obesa* showing a complex pattern of components. Two shoulders are evident along the left side of RT 14.21 and another shoulder is present to the right of RT 15.44. RT 6.21 is IS.—4. Profile of *E. obesa* cristata showing the sample profile as in the normal *E. obesa* plant. RT 16.24 is IS.—5. Profile of *E. susannae* showing the characteristic peak pattern. A shoulder is evident to the right of RT 14.41. RT 6.33 is IS.—6. Profile of *E. nivulia* showing the four distinctive peaks. The profile of this taxon resembles *E. lactea* but differs qualitatively for the ratios of component triterpenoids. RT 6.5 is IS.

dissimilar stock plants and grown at these two different sites, possess identical profiles (Figs. 5, 6; Table 1). Collection time also shows no change in profile composition; samples collected for both taxa were prepared at different times of the year.

Approximately 15 triterpenoid compounds are present in the plants and are expressed as different retention times (Table 1). The RT values are expressed as percent composition of the prominent components present in the latex. The triterpenoid distribution varies among the taxa. For example, those compounds represented by RT values 15.31 and 16.71 are present in five taxa, while other compounds are distributed among four or fewer taxa. A compound, as represented by RT 15.12, occurs in only one taxon, *E. ledienii* (Table 1). Coinjection of standards with extracts from both normal and cristata forms provide preliminary information of several components in the profiles including ergosterol (RT 12.80), campesterol (RT 13.13), stigmasterol (RT 13.68), and α-amyrin (RT 15.31). Other studies directed specifically to isolation and subsequent spectral analyses of isolates will provide identification of each compound.

The triterpenoids represent the prominent class of compounds present in the acetone extract of latex. Other substances such as the polyisoprenoid and proteinaceous contents are precipitated in the acetone extract. Few low molecular weight (below RT 12.00) or high molecular weight (above RT 18.00) compounds are present in the latex extract.

The quantitative data for each corresponding peak pair between the normal and cristata forms for each taxon were examined statistically with the Wilcoxon matched-pair signed-ranks test. These analyses indicated no significant difference (0.05% significance level) in the percentage composition for the compounds between pairs of peaks for each RT value in normal and cristata plants.

Discussion

Data from these chromatographic analyses of latex components show the triterpenoid profiles from both normal and cristata plant pairs to remain quantitatively and qualitatively comparable for a given taxon. The morphogenetic changes leading to the cristata condition on a given plant do not alter the physiological mechanism associated with the biosynthesis of triterpenoids in the laticifer. Similarly, the profile remains stable for samples collected from specimens of plant pairs derived from different origins, grown at different geographical locations, and sampled at different times of the year. Thus, laticifer triterpenoid composition remains stable under diverse morphogenetic and environmental conditions.

In other higher plants such as *Solanum* and *Nicotiana* the sterolic triterpenoid composition of tissues is reported to change during growth and in response to different environmental conditions (Bae & Mercer, 1970; Bush & Grunwald, 1972; Grunwald, 1975). The noted comparative stability for triterpenoid profiles in laticifers of *Euphorbia* taxa is in marked contrast to reported changes in content of similar compounds in other plants.

The triterpenoid synthesizing mechanism in the *Euphorbia* laticifer, in contrast to other cells of the plant, has evolved a high level of stability both for the types of triterpenoids and for the relative ratio of these different compounds produced in a taxon. Their stability in the laticifer may relate to the unique embryonal origin and intrusive growth pattern of this cell during plant development (Mahlberg & Sabharwal, 1968). Because the laticifer remains cytologically isolated from the shoot meristem during postembryonal growth, whereas other tissues continuously derive cells from the meristem, the metabolic activity of the laticifer could differ from that of other tissues.

The potential taxonomic value of triterpenoids from *Euphorbia* latex was recognized in previous studies (Anton, 1974; Ponsinet & Ourisson, 1965, 1968). More recent studies emphasize the distinctive character of a triterpenoid profile, which is described as a fingerprint for the taxon (Mahlberg & Pleszczynska, 1983; Mahlberg et al., 1983). The stability demonstrated for this triterpenoid profile in the laticifer in both normal and cristata forms of a taxon indicates that this trait is conserved under abnormal morphogenetic conditions of growth and lends additional support to the concept that the triterpenoid profile represents a fingerprint for a taxon.

These fingerprints therefore have application for identifying specific cristata forms that are dissimilar from the normal plant, as well as distinguishing between these forms for different taxa. In summary, the stability of the laticifer triterpenoid profile in abnormal and normal plant pairs of several taxa examined under diverse conditions supports an interpretation that these distinctive profiles can be employed as an additional

and important taxonomic character for studies of the genus *Euphorbia*.

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PRINCIPALES DISTRIBUTIONS OBTENUES PAR L'ANALYSE FACTORIELLE DES ÉLÉMENTS PHYTOGÉOGRAPHIQUES PRÉSUMES ENDÉMIQUES DANS LA FLORE DU ZAÏRE

M. NDJELE[1]

RÉSUMÉ

Le présent travail constitue une mise en évidence des principaux types d'aires de distribution des plantes supérieures endémiques au Zaïre. Les cartes de distribution de 1.100 taxons ont été dessinées à l'aide d'un programme informatisé. Par ailleurs, la carte du Zaire a été surchargée d'une grille de 839 mailles représentant un quart-degré chacune. Ces carrés ont été comparés entre eux quant à leur contenu floristique à l'aide d'une analyse factorielle; par l'union des carrés semblables, on obtient des principaux types de distribution. Pour chaque type d'aire, des exemples de taxons ont été cités.

ABSTRACT

The present study analyzes the principal types of distribution of higher plants endemic to Zaire. Distribution maps of 1,100 taxa have been drawn with the aid of a computer program. Furthermore, the map of Zaire has been overlaid with a grid of 839 sectors each representing a quarter degree. The floristic content of each of these sectors has been compared using factorial analysis; by joining similar sectors, the principal types of distribution can be obtained. For each type of distribution, example taxa are cited.

Avant d'utiliser les "espèces" dans les recherches phytogéographiques, il convient d'abord de s'assurer des déterminations parce que les faits phytogéographiques peuvent être influencés par le traitement taxonomique des plantes. A ce point de vue, signalons que notre échantillon est principalement constitué des espèces appartenant aux familles publiées dans la Flore d'Afrique Centrale (Zaïre). Il est vrai qu'au fur et à mesure de l'état d'avancement de la connaissance de la botanique zaïroise, différents auteurs ont fait au cours de ces dernières années, de nombreuses contributions sous forme de révisions. Dans cette étude, nous considérons comme espèce "endémique du Zaïre" toute espèce dont l'aire de distribution se trouve entièrement comprise à l'intérieur de ce territoire. Pour information, le territoire du Zaïre s'étend sur une superficie totale de 2.344.885 km^2 entre les parallèles 5°20′N et 13°28′S et les méridiens 12°10′ et 31°15′E. Parmi les espèces étudiées, il y en a qui ont une distribution limitée à une partie du territoire; d'autres ont une étendue plus ou moins large à l'intérieur du même territoire; enfin certaines ne sont connues que par un ou deux localités.

En réalité le Zaïre ne constitue pas à lui seul une grande unité chorologique. Il est à cheval sur plusieurs régions dont les principales sont la région Guinéo-Congolaise et la région Soudano-Zambézienne, reconnues par divers auteurs (Lebrun, 1947; Monod, 1957; Aubréville, 1962; Léonard, 1965; Troupin, 1966; Trochain, 1969; Brenan, 1978; White, 1971, 1976). White (1979) pense que la région Soudano-Zambézienne doit être considérée comme "région" au sens large ou "super région"; il y reconnaît une région Soudanienne et une région Zambézienne. Il en est de même de Denys (1980). D'autres subdivisions existant au Zaïre et reconnues par ces mêmes auteurs sont la Région Afro-Alpine ou "Afromontane Region," dans les montagnes du Kivu à l'est du Zaïre, et les deux zones de transition, l'une Guinéo-Congolaise/Soudanienne à l'extrême nord du Zaïre, et l'autre Guinéo-Congolaise/Zambézienne au sud du Zaïre.

Pourquoi avoir choisi d'étudier les espèces au lieu de taxons supérieurs? Nous pensons que l'utilisation de la distribution des genres et familles pour le territoire du Zaïre ne peut pas aboutir à des conclusions intéressantes. Afin d'obtenir une structure chorologique stable et objective il semble, d'après White (1979), qu'on puisse se tourner vers les espèces. Les modèles de distribution montrés par les espèces, et spé-

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cialement les espèces endémiques, sont frappants (White, 1976, 1978, 1979).

Pour le Zaïre, Robyns (1948) a proposé les territoires phytogéographiques floristiques sur base des formations végétales et de bioclimat (hauteur des précipitations, longueur de la saison sèche). Ces territoires, appelés Districts, se repartissent de la manière suivante: Dix districts au Zaïre (I. Côtier; II. Mayumbe; III. Bas-Congo; IV. Kasaï; V. Bas-Katanga; VI. Forestier Central; VII. Ubangi-Uele; VIII. Lac Albert; IX. Lacs Edouard et Kivu; XI. Haut-Katanga); le onzième District s'étend sur le Rwanda et le Burundi (X. Ruanda-Urundi).

Nous signalons ici, pour des raisons politico-administratives, des modifications relatives aux changements des noms des lieux intervenus dans notre pays. Il faut noter que cette dénomination intervenue ne change pas les limites géographiques des districts reconnus: ainsi Bas-Congo est devenu Bas-Zaïre, Bas-Katanga est devenu Bas-Shaba, Lac Albert est devenu Lac Mobutu Sese Seko, Lacs Edouard et Kivu est devenu Lacs Amin Dada et Kivu.

La notion d'endémisme, qui est pourtant essentielle à la phytogéographie et fondamentale pour la reconnaissance des unités phytogéographiques, n'y a pas été développée. D'ailleurs Robyns (1948) reconnaît que son système constitue une division provisoire.

Les résultats présentés dans ce travail complètent et précisent ces travaux antérieurs.

Matériels et Méthodes

Pour établir la distribution des espèces, nous avons utilisé les ressources de la littérature et celles des herbiers, principalement ceux déposés au Jardin Botanique National de Belgique (Meise) qui peut recéler le maximum d'herbiers en provenance du Zaïre.

Une carte reprenant les contours du territoire du Zaïre a été dessinée sur ordinateur. Les coordonnées géographiques des lieux de récolte sont introduites. Une base de données est créée en mémorisant les données qui se rapportent aux différentes espèces. L'appel d'un programme informatisé permet de sortir automatiquement pour chaque espèce, une carte du Zaïre à l'intérieur de laquelle sont dirrectement positionnés, les points correspondant aux localités de récolte. Chaque carte est accompagnée de renseignements suivants: nom d'espèce et nom de famille. Mille-cent cartes ont été ainsi dessinées; elles sont consultables au Laboratoire de Botanique Systématique et de Phytosociologie, Professeur J. Lejoly. Parmi les espèces étudiées, certaines ont été déjà publiées avec des cartes de distribution. Elles sont citées dans l'index des cartes de répartition des plantes vasculaires d'Afrique, établi par Lebrun & Stork (1977).

Par ailleurs, la carte du Zaïre a été surchargée d'une grille de 839 mailles représentant ¼ de degré chacune. Ces carrés ont été comparés entre eux quant à leur contenu floristique. Dans le but de trouver une relation entre ces carrés, l'analyse factorielle a été utilisée suivant une méthode mise au point par Petit & Symons (1974) et par Denys (1980). Par l'union des carrés semblables, on obtient des types d'aires de distribution.

Principales Distributions Observées et Éléments Endémiques

Les Figures 1, 2 et 3 illustrent la méthode de la cartographie spécifique. Les exemples choisis sont les cartes de distribution de quelques espèces intéressantes et caractéristiques des types d'aires déterminés.

La méthode de l'analyse factorielle a permis de retenir 10 types d'aires de répartition suffisamment distincts. Les aires géographiques déterminées peuvent être observées à la Figure 4.

Éléments phytogéographiques endémiques guinéo-congolais

1. Distribution prépondérante dans le nord du Secteur Forestier Central, avec une irradiation dans l'ouest. Exemples: *Beilschmiedia leemansii, Croton pynaertii, Rhabdophyllum thonneri, Deinbollia laurentii, Placodiscus pynaertii,* et *Cola selengana.*

→

Figure 1. Distribution au Zaïre de quelques espèces endémiques guinéo-congolais.—a. Espèce à distribution limitée principalement dans le nord du secteur Forestier Central.—b. Espèce distribuée dans le sud-ouest du Forestier Central, se retrouve aussi aux environs de Kinshasa.—c. Espèce à distribution limitée au centre et à l'est du Forestier Central.—d. Espèce distribuée dans le sud du Forestier Central et le nord du Kasaï.—e. Espèce à distribution limitée aux plateaux et vallées du Kwango.—f. Espèce à distribution large dans la partie guinéo-congolais du Zaïre.

Ochnaceae
Rhabdophyllum thonneri

Caesalpiniaceae
Crudia harmsiana

Annonaceae
Atraguatteria bequaertii

Fabaceae
Dalbergia gentilii

Anacardiaceae
Ozoroa kwangoensis

Myrtaceae
Syzygium giorgii

FIGURE 2. Distribution au Zaïre de quelques espèces endémiques orientales. — g, h, i. Espèces caractéristiques de la dorsale occidentale inférieure du Kivu. — j, k, l. Espèces principalement distribuées dans les montagnes du Kivu.

FIGURE 3. Distribution au Zaïre de quelques espèces endémiques zambéziennes.—m, n, o. Espèces caractéristiques des sols empoisonnés par les métaux lourds.—p, q, r. Espèces caractéristiques des hauts plateaux du Shaba.

FIGURE 4. Types d'aires de répartition des espèces endémiques.—1. Distribution dans le nord du secteur Forestier Central.—2. Distribution principale dans le sud-ouest du Forestier Central avec une disjonction au Bas-Zaïre.—3. Distribution planitiaire dans le centre et l'est du Forestier Central.—4. Distribution prépondérante dans le sud du Forestier Central et le nord du Kasaï, parfois avec une irradiation au Kwango et dans l'ouest du Forestier Central.—5. Distribution principale sur les plateaux du Kwango et les vallées environnantes.—5'. Distribution large, c'est-à-dire recouvrant les distributions 1, 2, 3, 4, et 5.—6. Distribution dans la partie de la dorsale occidentale du Kivu, parfois avec des irradiations en plaine.—6'. Distribution sur les hautes altitudes des montagnes du Kivu (sur la carte, se superpose à la distribution 6).—7. Distribution sur les hauts plateaux du Shaba.—8. Distribution sur les sols empoisonnés par les métaux lourds.—9. Absence d'espèces endémiques ou parties du territoire mal explorées sur le plan botanique. Limites des régions, d'après White (1979): |||| région Guinéo-Congolaise; ∧ ∧ ∧ ∧ région Zambézienne; × × × × région Montagnarde.

2. Distribution principale dans le sud-ouest du Secteur Forestier Central avec parfois une disjonction vers le Bas-Zaïre. Exemples: *Uvaria pynaertii, Polygala gilletiana, Cissus lebrunii, Millettia exauriculata, Tilliacora ealaensis,* et *Anisocycla cymosa.*

3. Distribution planitiaire dans de centre et l'est du Secteur Forestier Central. Exemples: *Combretum capitatum, Afraguatteria bequaertii, Gilbertiella congolana, Uvaria rivularis, Rhabdophyllum refractum, Xylia ghesquierei,* et *Baphia dubia.*

4. Distribution prépondérante dans le sud du Secteur Forestier Central et le nord du Kasaï. Exemples: *Enantia ambigua, Cissampelos tenuipes, Garcinia lujae, Pseudoprosopis uncinata, Millettia sapinii,* et *Dalbergia gentilii.*

5. Distribution principale sur les plateaux du Kwango et les vallées environnantes. Exemples: *Triclisia lanceolata, Oxygonum vanderystii, Ozoroa kwangoensis, Trichoscypha kwangoensis, Agelaea poggeana, Crotalaria vanderystii,* et *Leptoderris gilletii.*

5'. Distribution large, c'est-à-dire recouvrant les distributions 1, 2, 3, 4 et 5. Exemples: *Beilschmiedia variabilis, Coelocaryon botryoides, Cola bruneelii, Allanblackia kisonghi, Leptoderris laurentii, Syzygium giorgii,* et *Pentadesma exelliana.*

ÉLÉMENTS PHYTOGÉOGRAPHIQUES ENDÉMIQUES ORIENTAUX

6. Distribution dans la partie occidentale inférieure de la dorsale du Kivu, parfois avec des irradiations en plaine. Exemples: *Camptostylus kivuensis, Cleistanthus pierlotii, Rinorea mildbraedii, Craterosiphon beniense, Sorindeia multifoliolata, Pentadesma lebrunii, Impatiens masisiensis.*

6'. Distribution sur les hautes altitudes des montagnes du Kivu, avec certaines descentes sur les Marungu (Hauts plateaux du Shaba). Exemples: *Beilschmiedia olivacea, Bersama mildbraedii, Impatiens erecticornis, Impatiens prainiana, Rinorea tshingandaensis.*

ÉLÉMENTS PHYTOGÉOGRAPHIQUES ENDÉMIQUES ZAMBÉZIENS

7. Distribution sur les hauts plateaux du Shaba (Biano, Kibara, Kundelungu, Manika, Marungu). Exemples: *Gnidia quarrei, Gnidia kundelunguensis, Protea kibarensis, Sebaea hockii, Triumfetta marunguensis, Tephrosia manikensis,* et *Drosera katangensis.*

8. Distribution sur les sols riches en métaux lourds. Exemples: *Gladiolus robiliartianus, Crotalaria cobalticola, Triumfetta likasiensis, Thesium thamnus, Gladiolus ledoctei,* et *Gladiolus actinomorphanthus.*

Discussion

L'interprétation du découpage obtenu n'est pas aisée. Il y a par exemple les aires constituées par les éléments orientaux, c'est-à-dire dans la partie occidentale de la dorsale du Kivu et dans les montagnes environnantes, qui apparaissent erronément sur le même plan de papier, alors qu'en réalité on les retrouve à des altitudes différentes.

La comparaison de ces entités aérotypiques avec les subdivisions antérieures établies par d'autres chercheurs a montré qu'un certain nombre d'entre elles, ont déjà été signalées:

Evrard (1965), établissant une statistique phytogéographique de la flore du Secteur Forestier Central, a conclu entre autres qu'au niveau spécifique, la flore de ce secteur peut être localement bien endividualisée; il a reconnu neuf types d'aires dont six ont été reconnus également dans ce travail.

Léonard (1965), dans sa contribution à la subdivision phytogéographique de la région Guinéo-Congolaise d'après la répartition géographique d'Euphorbiacées d'Afrique tropicale, pour la partie située au Zaïre, a reconnu cinq types d'aires; tous ont également été reconnus dans ce travail.

Duvigneaud & Denaeyer-De Smet (1963) a fait une première synthèse sur la distribution des plantes métallicoles du sud du Zaïre. Cette synthèse a été enrichie par Malaisse (1983) et s'insère géographiquement bien dans l'aire des éléments endémiques zambéziens.

Les détails concernant la plupart des espèces orientales et leur répartition dans les différentes montagnes et étages de végétation peuvent être trouvés dans Liben (1962).

Conclusion

Il est intéressant de noter que les résultats de ce travail, qui se limite aux types d'aires de distribution des plantes endémiques du Zaïre, avec ceux des travaux antérieurs précités, sont largement concordants et présentent beaucoup d'affinités avec les centres d'endémisme proposés par White (1978) et dont la végétation peut être reconnue sur la nouvelle carte AETFAT de la végétation de l'Afrique (White, 1983). Le problème des limites précises de ces aires n'a pas été abordé. Pour donner une idée de leur insertion au sein des subdivisions existantes, nous avons dessiné à la Figure 4 les limites des régions d'après White (1979).

Nous devons pourtant reconnaître que les aires géographiques déterminées, sont fonction du degré d'explorabilité botanique du territoire du Zaïre, ainsi qu'en témoigne la carte établie par

Hepper (1979). Enfin ce travail augmente les connaissances sur la distribution des plantes vasculaires d'Afrique tropicale, déjà entreprise par Lebrun (1981).

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PATTERNS OF SPECIATION IN AFRICA, MADAGASCAR, AND THE TROPICAL FAR EAST: REGIONAL FAUNAS AND CRYPTIC EVOLUTION IN VERTEBRATE-DISPERSED PLANTS[1]

C. M. Pannell and F. White[2]

Abstract

The two most famous faunal boundaries in the world, the Mozambique Channel and Wallace's Line, are described in terms of their geological histories. Four plant taxa (*Aglaia, Parinari,* and the *Diospyros ferrea* and *Hirtella zanzibarica* species complexes) that transcend these boundaries are considered, and the fruit-eating vertebrate faunas on the two sides of each of them are briefly compared. Variation in the fruits of some closely related vertebrate-dispersed plants, both allopatric and sympatric, including those mentioned above, are then described in greater detail in relation to the animals that are known or thought to disperse them. The term *cryptic evolution* is used to refer to divergence in features of taxonomic and ecological importance that had previously escaped detection. The paper considers how geological and especially tectonic events in different parts of the world have resulted in major regional differences in faunas. Some regional differences in floras, including floristic richness and patterns of speciation, are examined in the light of the faunal differences. The possible role of faunal extinctions, and the effects of geological history on the physical environment are also discussed. Examples are given that show how a knowledge of vertebrate dispersal can lead to improvements in taxonomy. Suggestions are made for overcoming our present lack of information on fleshy fruits and their dispersers.

Résumé

Les auteurs décrivent les deux limites faunistiques les plus célèbres du monde, le Canal de Mozambique et la ligne de Wallace au travers de leur histoire géologique. Quatre taxons de plantes (*Aglaia, Parinari* et les complèxes d'espèces de *Diospyros ferrea* et *Hirtella zanzabarica*) qui transcendent ces frontières sont considérées et les auteurs comparent la faune des vertébrés consommateurs de fruits des deux côtés de ces frontières. La variation dans les fruits de plantes très voisines et dispersées par des vertébrés, à la fois allopatriques et sympatriques, y compris celles mentionnées ci-dessus, sont ensuite décrites en détail en rapport avec les animaux qui les dispersent ou sont supposés le faire. Le terme évolution criptique est l'expression utilisée pour parler de la divergence de caractères d'importance taxonomique et écologique qui n'avaient pas été détectés jusque-là. Dans cet article les auteurs examinent comment des événements géologiques et surtout tectoniques ayant eu lieu dans diverses parties du monde ont entraîné des différences régionales importantes au niveau de la faune. Des différences régionales en ce qui concerne la flore, y compris la richesse floristique et les schémas de spéciation, sont examinés en vu des différences dans la faune. Les auteurs parlent aussi du rôle possible des extinctions faunistiques et des effets de l'histoire géologique sur l'environnement physique. Des exemples démontrent qu'une connaissance de la dispersion par les vertébrés peut conduire à des progrès en taxonomie. Des suggestions sont faites pour améliorer notre connaissance actuelle concernant les fruits charnus et leurs agents de dispersion.

If for instance a number of species which stand in direct competition with each other migrate in a body into a new and afterwards isolated country, they will be little liable for modification; for neither migration nor isolation in themselves can do anything.

Species occasionally arriving after long intervals . . . and having to compete with new associates will be eminently liable to modification and will often produce groups of modified descendants (Darwin, 1859: 351, 390).

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It is widely known that Africa, at least at the species level, is floristically poor compared with other parts of the tropics (Richards, 1973; Brenan, 1978) and that some animal groups, e.g., the birds (Snow, 1981), have fewer species. Africa is said to be the "odd man out"—a kind of poor relation. Its poverty is thought to be due to wholesale decimation in the Pleistocene. It is true that some plant groups such as the orchids and palms are poorly represented in Africa compared with other parts of the tropics, but, in placing too much emphasis on the species and by not taking ecological differences sufficiently into account, a somewhat distorted picture may be produced. Two examples can be used to illustrate this. (1) Hall & Swaine (1981: 31–32) have suggested that when entire floras of lowland tropical rain forest are compared, e.g., between Ghana and Malaya, the differences in floristic richness at the species level might be explicable in purely climatic terms. (2) Differences in species richness sometimes conceal other, possibly more important aspects of diversity. This is the case in the family Chrysobalanaceae (Prance & White, 1988). Of the 494 known species of Chrysobalanaceae, 385 occur in the Neotropics, only 61 in Africa, and 50 in the Far East, but Africa has 10 genera (5 endemic) compared with 8 (3 endemic) in the Americas; the Far East, despite its poverty in species, is also relatively diverse at the generic level (7 genera, 4 endemic).

We believe that in trying to understand regional differences in floras it is useful to consider other aspects of their histories as well as the possible effects of Pleistocene climatic change. Different parts of the tropics have had very different geological, especially tectonic, histories and at least some of their floristic and faunal peculiarities are a reflection of this. We explore here the possibility that geological history, with its resulting differences in fruit-eating vertebrate faunas in different parts of the world, might have contributed to regional differences in floras, including species richness and patterns of relationship between closely related taxa.

Regional variation in the fruits of widespread species and species complexes in relation to their dispersers in different parts of their geographical range is a subject that has hitherto received little attention, although a start has been made with some sympatric species (Pannell & Koziol, 1987; Dowsett-Lemaire, pers. comm.; J. A. & T. B. Hart, pers. comm.).

We later describe what is known of the fruits and of their dispersal in several species groups and genera. These belong mainly to three pantropical woody families—Chrysobalanaceae, Ebenaceae, and Meliaceae. We suggest some possible explanations for the taxonomic complexity in these groups and make some suggestions for future research. We use *cryptic evolution* to refer to divergence in features of taxonomic and ecological importance that have largely escaped detection so far.

Major Faunal Boundaries in the Old World

Geological background

At least since the early years of the nineteenth century, botanists and zoologists have divided the world into regions according to the distribution of plants and animals. The six regions of Sclater (1858), based on the distribution of birds, still stand today with little modification, even though they were published as evidence for the existence of six separate centers of divine creation in different parts of the world. Sclater's regions have also proved useful for other animal groups. It is now known that these regions broadly correspond to land masses that formerly were part of a supercontinent Pangaea. Their separation during the breakup of Pangaea was due to crustal movements that are now well documented chronologically, although the underlying mechanism is not yet fully understood (Wylie, 1976; Hallam, 1981; Smith et al., 1981; Windley, 1984). The fragments of Pangaea formed the cores of new tectonic plates and continued to move apart because of the accretion of new oceanic crust derived from volcanic activity along the oceanic ridges.

The main continental blocks including Antarctica, as well as some smaller continental fragments such as New Zealand, New Caledonia, Madagascar, and the Seychelles, have been isolated at least intermittently from other land masses for tens of millions of years. Some blocks such as Madagascar have remained isolated since the time of their separation, whereas others such as the Australo–Papuan fragment of Gondwanaland and the southeastern extremity of Asia have drifted towards each other; their collision began 15 Ma, continuing for the next 10 million years. New Guinea itself began to form somewhat earlier, following the collision of the Australian and Pacific plates in the late Eocene. These collisions resulted in widespread subduction, vulcanism, mountain building, and the repeated emergence

and submergence of continental crust (Hamilton, 1979; Audley-Charles, 1981; Audley-Charles et al., 1981; Pieters, 1982; Axelrod & Raven, 1982).

THE MOZAMBIQUE CHANNEL

By the late Cretaceous, the separation of Madagascar from the African mainland was complete, and there is no generally accepted geological evidence that they have been in contact at any time since then. At its narrowest the Mozambique Channel is approximately 400 km wide and its depth exceeds 1,000 m for a width of at least 100 km along its entire length. The volcanic Comoro Islands could have acted as "stepping stones" for some animals and plants, although the widest water gaps there are still almost as wide as the Mozambique Channel at its narrowest point. Further south, coral islands such as Juan de Nova and submerged sea mounts, which might now represent the remnants of former exposed volcanoes, could also have played a similar role. The high degree of endemism and the disharmonic nature of the Malagasy flora and fauna are compatible with a long period of isolation.

There are no strictly freshwater fishes in Madagascar, and several important groups of amphibians and reptiles are also lacking. Birds (Milon et al., 1973; Benson, 1984) and mammals (Paulian, 1984) are poor in species but rich in endemic genera and families. Zoologists (e.g., Darlington, 1957; Kingdon, 1979: 200, pers. comm.) believe that the existing Malagasy fauna could have been derived by dispersal across salt water. It is also possible that the three endemic families of lemurs have been derived from a single common ancestor. The largest mammal known to have reached Madagascar is the now extinct pygmy hippopotamus (*Hippopotamus lemerlei*), which was abundant in the Pleistocene. Of the 8,500 species of vascular plants known from Madagascar, 7,900 are phanerogams, of which 81% are endemic, as are eight families (Humbert, 1959; White, 1983a).

WALLACE'S LINE AND WALLACEA

Wallace first described his famous line in 1860 but had already mentioned it in January 1858 in a letter to Henry Bates (George, 1981). It was not named as such until 1868 (by Huxley). Wallace located it in the Strait of Lombok (separating Bali and Lombok), and although the water barrier is only 24 km wide, he showed that the faunas to the east and west of it are more distinct and contrasting than those of any other of the great zoological divisions of the globe. Wallace's Line separates the rich Oriental freshwater fish, amphibian, bird, and mammal faunas from the impoverished ones of Sulawesi (formerly Celebes) and the Lesser Sunda Islands (with their partial Australo–Papuan affinities) to the east (Keast, 1983).

Wallace (1863) was well aware of the significance of geology in relation to the faunal patterns of the Malay Archipelago. He knew that "one large portion of it is connected by a very shallow sea to the continent of Asia, another part is similarly joined to Australia, while the remaining islands are surrounded by a practically unfathomable sea." Since 1928 the name Wallacea (refs. in Keast, 1983) has been given to "the remaining islands" and the seas surrounding them (Fig. 1). It usually excludes the Philippines (e.g., map 2 in White & Bruce, 1986) but sometimes encompasses them.

Tables 1 and 2, in conjunction with Figures 1–4, show the distribution of certain plant and animal taxa in relation to Wallace's Line and Wallacea. More examples are given by Keast (1983). The significance of Wallace's Line and Wallacea varies among taxonomic groups. It is of limited importance as a division line or transition zone in plants (van Steenis, 1979) and insects (Gressitt, 1961). Keast attributes this to the different dispersal capacity of the groups, whereas other workers, e.g., Ashton (1982: 249) quoting Merrill (1923), find it "necessary to postulate continuous land connections from India to New Guinea" in order to explain the distribution of the plant family Dipterocarpaceae, since its fruits are usually dispersed only over short distances.

VERTEBRATE-DISPERSED PLANT TAXA THAT TRANSCEND FAUNAL BOUNDARIES

THE PANTROPICAL GENUS *PARINARI* (CHRYSOBALANACEAE)

Parinari, with 44 species, is widely distributed in tropical America, Africa, and Asia and extends eastwards to northern Queensland and Fiji, Tonga, and Samoa (Prance & White, 1988). The genus is remarkably uniform in the structure of its leaves, flowers, and fruits and is very easy to recognize. Most of the species look distinct in the field, but in the past there has been much confusion in herbaria.

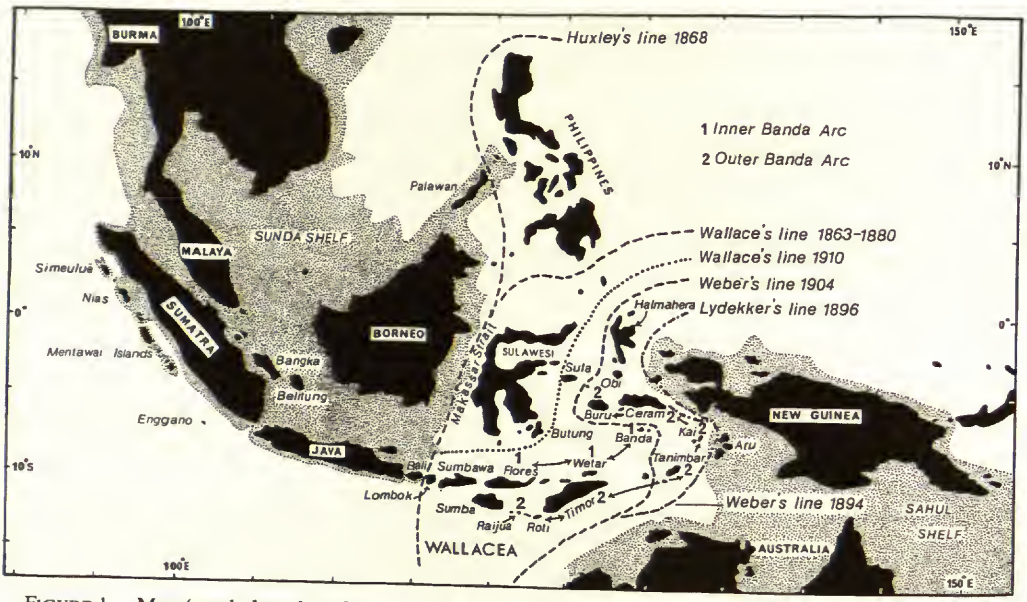

FIGURE 1. Map (partly based on figs. 2.1, 2.4, 4.7, and 4.9 in Whitmore, 1981), which in conjunction with Table 1 shows the distribution of certain plant and animal taxa in relation to the Sunda Shelf, Wallacea, and the Sahul Shelf.

THE PALAEOTROPICAL SPECIES-COMPLEX *DIOSPYROS FERREA* (EBENACEAE)

The latest monographer of Far Eastern Ebenaceae (Bakhuizen, 1936, 1941) interpreted this species in a wide sense; according to him it extends sporadically throughout the Old World tropics from Senegal to Hawaii (Figs. 5, 6). Except for some littoral species, it is probably more widely distributed than any tropical tree other than *Dodonaea viscosa* and *Gyrocarpus americanus* (White, 1983c: fig. 7), both of which are dispersed at least in part by ocean currents.

Diospyros ferrea is extremely variable, especially in the shape and size of its leaves and fruits, but, at least in the herbarium, variation appears to be highly reticulate and quasi-continuous and major geographical trends are not apparent. White (1962: 79) referred to it as an ochlospecies. Some authors of local studies recognize more than one species in this complex and most workers (including Bakhuizen) subdivide *D. ferrea* into sev-

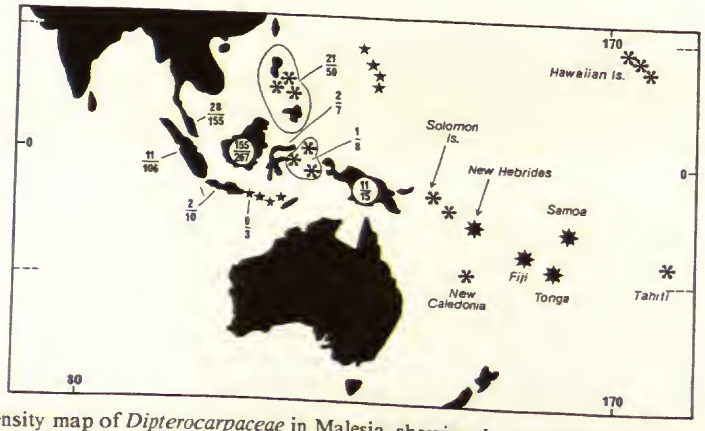

FIGURE 2. Density map of *Dipterocarpaceae* in Malesia, showing the number of endemic species above the line and the total number of species below (after Ashton, 1982).

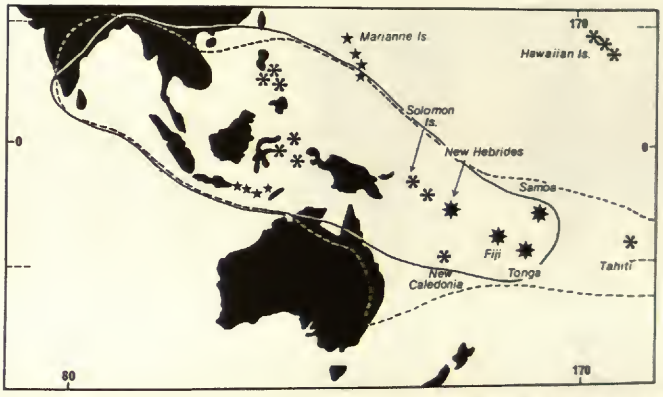

FIGURE 3. Approximate distributions of *Aglaia* (continuous line) and two genera of fruit-eating pigeons, *Ducula* and *Ptilinopus* (broken line).

eral infraspecific taxa, but there is much disagreement between the different accounts, e.g., Fosberg (1939) for Hawaii, Green (1969) for Melanesia, Smith (1971, 1981) for Fiji, Samoa, and Tonga, and Kostermans (1981) for Ceylon. In the absence of field studies from representative localities throughout the range of the complex, its taxonomy may never be satisfactorily resolved. Some of the variation appears to be related to local ecological conditions, including the availability of potential seed dispersers, but the taxonomy is made difficult by the scattered occurrence throughout the Indo-Pacific area of phenotypes that closely resemble some African phenotypes. According to Green, the name *D. elliptica* should take precedence over *D. ferrea* if they are regarded as conspecific, but until the group has been comprehensively revised we prefer to use the more familiar name.

THE AFRO-MALAGASY SPECIES COMPLEX *HIRTELLA ZANZIBARICA* (CHRYSOBALANACEAE)

With the exception of this complex, the remaining 91 species of *Hirtella* are confined to the Neotropics (Prance & White, 1988). White (1976a: 276; 1976b: maps 287–292) regarded the East African and Malagasy populations as conspecific but with subspecific differentiation, the nominate subspecies occurring on the mainland and four others in Madagascar. Further work, however, has shown that the African and Malagasy plants differ in their fruits and may not be conspecific.

FIGURE 4. Map, which in conjunction with Table 2 shows the western and eastern limits of certain families and subfamilies of fruit-eating birds in the tropical Far East (partly after Williamson, 1981 and Firth & Davidson, 1945). Note: for some families the limits are approximate, e.g., cassowaries also occur in Ceram, and hornbills are absent from Australia.

TABLE 1. The distribution of certain taxa in relation to Wallace's Line and Wallacea (see Fig. 1).

Taxonomic Groups	Sunda Shelf	Wallacea	Sahul Shelf and Beyond
Placental mammals	Diverse	Very few	Only bats and rodents
Primates	Diverse, including two families of apes	Very few, e.g., one tarsier and three species of macaque. No apes	None
Marsupials	None	Very few, e.g., two endemic species of *Phalanger* in Sulawesi	Diverse, e.g., six families in New Guinea
Agathis	*A. dammara*	*A. dammara*	*A. dammara* in New Guinea, 10 species elsewhere
Araucaria	None	None	Several
Dipterocarpaceae	Numerous, e.g., 267 species in Borneo	Very few, e.g., seven species in Sulawesi	15 species (11 endemic) in New Guinea

THE FAR EASTERN GENUS *AGLAIA* (MELIACEAE)

Aglaia, with more than 100 species, is the largest genus in the pantropical mahogany family. It is confined to the eastern tropics and extends from India to Samoa and from China southwards to Queensland (Pannell & Koziol, 1987). *Aglaia* was placed by van Steenis (1969: 115) with those tropical Far Eastern genera whose species form "solid blocks." Although the species in such genera may be clearly defined, they are sometimes difficult to key out and "several often grow side by side without appreciable preference for distinguishable, separated ecological niches in extremely mixed primary rain forest." Subsequent fieldwork (Pannell, 1980; Pannell & Koziol, 1987) has partly resolved the pattern of taxonomic and ecological differentiation in *Aglaia* within peninsular Malaysia and Sumatra. In particular, differences in fruit structure and dispersal biology have been found to be important, although they remain poorly known for all but a few species.

THE DISTRIBUTION OF FRUIT-EATING VERTEBRATES ACROSS FAUNAL BOUNDARIES

THE MOZAMBIQUE CHANNEL

According to Moreau (1966: 340), the fruit-eating bird fauna of Madagascar is impoverished compared with that of the African mainland. Nevertheless, it is larger and more diverse than

TABLE 2. Western and eastern limits of the main families and subfamiles of fruit-eating birds in the tropical Far East in relation to the lines drawn on Figure 4.

A. WESTERN LIMITS

1. Between lines 1 and 2, Figure 4.
   Casuariidae (cassowaries), Paradisaeidae (birds of paradise), Ptilonorhynchidae (bower birds).
2. West of line 1, Figure 4.
   All other families.

B. EASTERN LIMITS

1. West of line 1, Figure 4.
   Capitonidae (barbets), Eurylaimidae (broadbills), Pycnonotidae (bulbuls).
2. Between lines 1 and 2.
   Casuariidae (cassowaries), Oriolidae (orioles), Paradisaeidae (birds of paradise), Ptilonorhynchidae (bower birds).
3. Between lines 2 and 3.
   Bucerotidae (hornbills), Dicaeidae (flower peckers).
4. Between lines 3 and 4.
   Corvidae (crows).
5. Between lines 4 and 5.
   Megapodiidae (brush turkeys), Turdinae (thrushes), Zosteropidae (white eyes).
6. Between lines 5 and 6.
   Sturnidae (starlings).
7. East of line 6.
   Columbidae (fruit pigeons), Muscicapinae (flycatchers), Sylviinae (warblers).

FIGURE 5. Pictorialized distribution map of *Diospyros ferrea* showing variation in shape and size of leaves and fruits in Africa (partly after White, 1978, fig. 5, and White, 1983b, fig. 55, where provenances of the illustrated leaves and fruits are given). The roman numerals refer to the regional phytochoria of White (1983a). Scale bars = 1 cm.

Moreau supposed (Dowsett-Lemaire, pers. comm.). In Madagascar there are no barbets (Capitonidae), hornbills (Bucerotidae), turacos (Musophagidae), or orioles (Oriolidae); the starlings (Sturnidae) and bulbuls (Pycnonotidae) are each represented only by a single species—*Sarcoglossa aurata*, the Madagascar starling, and *Hypsipetes madagascariensis*, the Madagascar bulbul. In addition to the starling and bulbul and one terrestrial *Coua* (Cuculidae), which apparently eats only fruits that have fallen to the ground, Moreau only mentions two species of the endemic genus *Philepitta* of the family Philepittidae (Asities) and two fruit pigeons (Columbidae), namely the Madagascar blue pigeon, *Alectroenas madagascariensis*, and the green pigeon, *Treron australis*. The latter is very closely related to the African green pigeon (*T. calva*), a widespread mainland species, and to two endemic insular species, *T. s. thomae* and *T. pembaensis*, which occur respectively on the island of San Tomé in the Gulf of Guinea and on Pemba Island, 40 km east of the coast of Tanzania (Goodwin, 1983). On present knowledge it is a matter of opinion whether these four species should be treated as members of a superspecies or as races of *T. australis* (Goodwin in Snow, 1978: 221). In this paper we follow the latter view.

To Moreau's list Dowsett-Lemaire would add the endemic Madagascar white-eye, *Zosterops*

maderaspatana (Zosteropidae), and the endemic Madagascar magpie robin, *Copsychus albospecularis* (Turdidae), both of which eat fruits, as do most and probably all of the nine species of the endemic genus *Coua*. The Blue Coua (*C. caerulea*) is arboreal and behaves very much like an African turaco. Fruits also feature in the diet of *Monias benschi*, Bensch's rail (Milon et al., 1973), a member of the small endemic family Mesitornithidae, which is thought to be allied to the true rails, cranes, and bustards. Seeds, possibly from fallen fruits, have been found in the stomach of the forest-dwelling wood rail (*Canirallus kioloides*), Rallidae; Rand, 1936; Milon et al., 1973).

Fruit-eating mammals are even less varied in Madagascar than the birds. There are four fruit bats (Kingdon, 1974; Sussman & Raven, 1978) and about half of the 26 living species of lemur have been recorded as eating at least some fruit (Jolly et al., 1984).

WALLACE'S LINE

The limits of distribution of the families of fruit-eating birds in the tropical Far East are summarized in Figure 4. Three families [the bulbuls, the barbets, and the broadbills (Eurylaimidae), which are implicated in the dispersal of *Aglaia* in West Malesia] do not reach New Guinea, whereas other families of fruit-eating birds such as the birds of paradise (Paradisaeidae), bower birds (Ptilonorhynchidae), and the flightless cassowaries (Casuariidae) do not occur to the west of Wallacea (Fig. 4). Fruit-eating pigeons are more diverse in New Guinea than elsewhere (Goodwin, 1983). New Guinea also lacks the large placental mammals that elsewhere forage terrestrially, and birds fill some of the roles not occupied by mammals. Hence, three species of cassowary, four genera of mound-building megapodes (Megapodiidae), three genera of large ground pigeons (*Trugon*, *Otidiphaps*, and *Goura*), one species of hornbill (Bucerotidae), and many smaller birds forage on the forest floor. *Trugon* and *Goura* apparently only eat fruit, but most of the others eat insects and even small vertebrates in addition to fallen fruits (Beehler, 1982).

Most species in four of the six marsupial families present in New Guinea are known or believed to include fruit in their diet (Ziegler, 1982), but details of their feeding habits and the fruits they eat are not known. These families are the Peramelidae (bandicoots), Phalangeridae (cuscuses or phalangers), Burramyidae (pygmy possums), and the Petauridae (striped and gliding possums, ringtails). Many of these species are arboreal and, compared with the birds, are probably relatively unimportant in dispersal. Bats, by contrast, almost certainly are important, although little is known of their role as dispersers in New Guinea. The fruit bat fauna of New Guinea consists of 26 species (in nine genera), of which half are endemic (Ziegler, 1982).

As Figure 4 shows, the variety of birds available for seed dispersal falls off rapidly to the east of New Guinea. The mammalian fauna is even more depleted. In Hawaii there are very few resident fruit-eating birds, and the only indigenous mammal is an insectivorous bat.

VARIATION IN THE FRUITS OF CLOSELY RELATED VERTEBRATE-DISPERSED PLANTS

AGLAIA

(1) *In Sundaland*

In those species of *Aglaia* occurring on the Sunda Shelf there are two main types of fruit. They are associated with two main types of vertebrate disperser, namely birds and primates (Pannell, 1980; Pannell & Koziol, 1987).

Bird-dispersed fruits. The fruit is a capsule and contains a few large, red, arillate seeds. The pericarp is brick red or pink on the outside and white inside, and the contrast in color of pericarp and seed makes the fruits conspicuous. The aril, which is high in lipid (27–60% dry weight in those species for which analyses have been made), can be easily separated from the rest of the seed, and this probably means that it is easily removed by the action of the gizzard or gut of the dispersing birds, which regurgitate or pass the seeds unharmed.

Field observations, mainly by C.M.P., suggest that the large-seeded dehiscent species of *Aglaia* are dispersed by hornbills and possibly fruit pigeons and that the smaller-seeded species are dispersed by hornbills and an array of smaller birds, including bulbuls, broadbills, and barbets. The small birds probably effect mainly local dispersal, but hornbills and pigeons are known to fly distances of 100 km or more and could be important in longer-distance dispersal.

Primate-dispersed fruits. The fruit is indehiscent and the pericarp is orange, pinkish-orange, or brown. The white, yellow, or orange, translucent aril is low in lipid but high in reducing sugars and sucrose and in sweet-tasting amino acids. Primates break open and peel off the

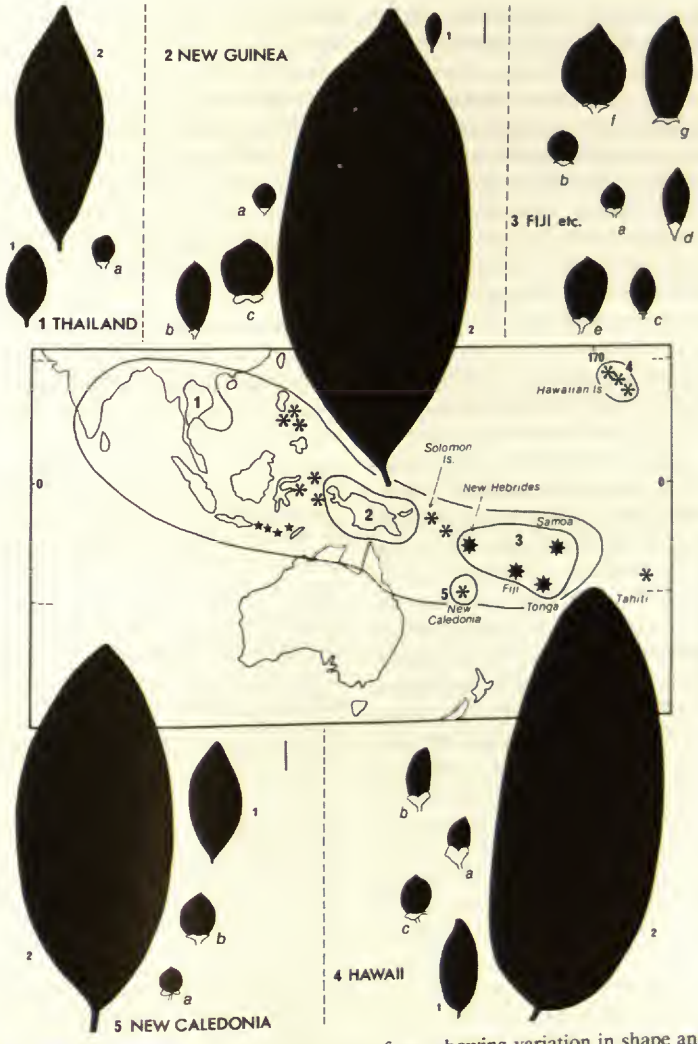

FIGURE 6. Pictorialized distribution map of *Diospyros ferrea* showing variation in shape and size of leaves and fruits in the tropical Far East. For four parts of its geographical range the largest and smallest leaves and and fruits in the tropical Far East. For four parts of its geographical range the largest and smallest leaves and the range in fruit shape and size are shown. For area 3, only the fruits are illustrated. The provenances of the specimens illustrated are given in an unpublished typescript available on request from the authors. Scale bars = 1 cm.

pericarp and either swallow the seed plus aril whole or suck off the aril and discard the seed. The aril adheres firmly to the testa and this, together with its gelatinous nature, probably encourages primates to swallow the seed or carry it away before eating the flesh.

At least two species of monkey (*Presbytis melalphus* and *Macaca fasicularis*) and three species of ape, namely the orangutan (*Pongo pygmaeus*), the siamang (*Hylobates syndactylus*) and the white-handed gibbon (*H. lar*), ingest the seeds of *Aglaia* in the areas where the study was carried out. A survey of the literature written by primatologists (summarized by Pannell & Koziol, 1987) indicates that primates are the principal dispersers of the indehiscent species.

Other possible dispersers. Other animals might occasionally effect dispersal, although they appear to be relatively unimportant. Squirrels are mainly destructive but occasionally disperse seeds over short distances. Terrestrial rodents and ground-feeding birds such as the crested

wood partridge (*Rollulus rouloul*) may play a similar role. Seeds of *Aglaia* cf. *elaeagnoidea* have been found in the feces of *Paradoxurus hermaphroditicus* (Viverridae, the civet family). Elephants, rhinos, tapirs, and some deer are known to feed on fallen fruits of other plant families and may also contribute to the dispersal of *Aglaia*. Bat dispersal is a possibility for some species.

(2) *East of Wallace's Line.*

Species of *Aglaia* with dehiscent and indehiscent fruits occur east of Wallace's Line but little is known about their dispersal compared with some of the Sundaland species; the absence of ripe fruits preserved in spirit means that the morphological features of dehiscence and aril type known to be associated with different types of disperser in Sundaland are also not available.

In the dehiscent group, fruit pigeons, which are implicated in the dispersal of *Aglaia* in the west (Wyatt Smith, 1953a, 1953b), may also be important in the east, since they are known to feed on *Dysoxylum* (Crome, 1975), a related genus with similar fruits and seeds. Indeed, pigeons may have transported the seeds of *Aglaia* species with capsular fruits across Wallace's Line. They might therefore have played an important part in bringing about the collective geographical range of *Aglaia*, which lies almost entirely within the area of distribution of *Ducula* and *Ptilinopus*, the principal genera of fruit-eating pigeons in the Far East (Fig. 3). It is highly likely, however, that other birds also disperse *Aglaia* seeds east of Wallace's Line. Beehler's observation (1983) that in New Guinea the arillate seeds of an unidentified species of *Aglaia* with dehiscent fruits feature in the diet of two birds of paradise, *Parotia lawesii* and *Paradisaea raggiana*, has been shown to be based on a mistaken identification of the plant, which almost certainly belongs to *Dysoxylum* (Pannell & Koziol, 1987). However, it seems likely that future field investigations will show that arillate seeds of *Aglaia* do feature in the diet of some birds of paradise. Beehler also found that the meliaceous *Chisocheton weinlandii* (*C. lasiocarpus* "entity" *weinlandii* of Mabberley, 1979: 334) was visited exclusively by birds of paradise, and all of the nine species occurring in the study area participated in the feast. Its "arillate seeds required some effort to harvest from their capsules" (p. 8). This might suggest that the precise manner of presentation of the seeds of *Chisocheton* is related to some structural and behavioral features of the birds of paradise and gives them an advantage over other potential dispersers.

Primates, which are important dispersers of the indehiscent species of *Aglaia* in Sundaland, are absent from Australasia. Their role in dispersal may be fulfilled by fruit-eating marsupials, rodents, bats, or ground-dwelling birds. For instance, Stocker & Irvine (1983) have shown that *Casuarius casuarius* feeds almost exclusively on fallen fruits including those of *Aglaia* ("*Amoora ferruginea*"), and seeds of this species collected from cassowary dung showed good germination (we have not yet checked their voucher specimens to confirm the identification of the species).

GUAREA CEDRATA AND *G. MAYOMBENSIS* (MELIACEAE)

The geographical range of *Guarea mayombensis*, which is sometimes given generic rank as *Leplaea*, lies entirely within that of *G. cedrata*. These two species are so similar in vegetative and floral characters that herbarium taxonomists have sometimes confused them (Pennington & Styles, 1975: 497). Their fruits, however, are markedly different. *Guarea cedrata* has a relatively small (4–5.5 cm diam.) capsule and its orange arillate seeds are presumably dispersed by birds as are those of other species, e.g., *G. glabra* (Howe & De Steven, 1979). In *G. mayombensis* the fruit is much larger (10–12 cm diam.) and does not dehisce on the tree. Some, but not all fruits show lines of weakness, and on striking the ground they may fall apart (Pennington & Styles, 1975), although this apparently is not normal (M. Cheek, pers. comm.). The very large seeds have a thin orange aril and are presumably dispersed by mammals. According to Cheek, in Uganda the "fruits" are relished by baboons. Butynski (pers. comm.) suggests primates (including baboons), elephants, and pigs as possible dispersers.

KLAINEDOXA (IRVINGIACEAE)

Most taxonomists recognize only one species, *Klainedoxa gabonensis*. It occurs more or less throughout the Guineo–Congolian rain forest region and is said to be dispersed by elephants (Alexandre, 1978). Ecologists in Gabon, however, recognize three fruit types which differ in color, shape, and size (Gentry, 1984). Gentry has shown that three widely distributed, largely sympatric species, namely *K. gabonensis*, *K. microphylla* and *K. trillesii*, are involved. The obser-

vations of J. A. and T. B. Hart in Ituri (pers. comm.) suggest that the differences in fruit may be related to the food preferences of different potential dispersers. They found the big green fruit of *K. gabonensis* sensu stricto in the rumen of the bay duiker (*Cephalophus dorsalis*), and other species of duiker would eat it in captivity. The slightly smaller yellow fruit of *K. trillesii,* by contrast, was rejected by all the duikers in their experiments. They also found the fruits of *K. gabonensis* and *K. trillesii* in elephant dung. Fruits of *K. gabonensis* have lower levels of condensed tannins and fiber and higher levels of nitrogen than have fruits of *K. trillesii*; in controlled tests, preference for fruits by duikers was positively correlated with nitrogen to fiber and tannin ratios.

PARINARI

Despite the apparent uniformity in the fruit of *Parinari,* it is known to be eaten and in some cases dispersed by a great variety of vertebrates (Prance & White, 1988), including fishes, bats, primates, squirrels, elephants, antelopes, flightless birds (rheas and emus), and flying birds (hornbills and fruit pigeons, including the green pigeon, *Treron australis* sensu lato).

In different parts of the geographical range of *Parinari,* a different spectrum of potential dispersers is available. No detailed studies have been made of the chemistry and precise structure of the fruits in relation to dispersal, but there are indications that certain species differ in these respects. In Kalimantan the orange fruit of *P. canarioides,* which has a white sugary mesocarp, is dispersed by three primates, Müller's gibbon (*Hylobates muelleri*), the orangutan, and the pigtailed macaque (*Macaca nemestrina*); it has the widest endocarp known to be swallowed and passed by primates (Leighton, pers. comm.).

In some parts of Africa the geographical range of the forest species *Parinari excelsa* overlaps with that of the savanna woodland species *P. curatellifolia* (White, 1976a, 1976b). Both species appear to be predominantly dispersed by mammals, but the fruits of *P. curatellifolia* are also known to be eaten by birds, and the seeds of *P. excelsa* are eaten by parrots. *Parinari excelsa* is dispersed by elephants (Alexandre, 1978) and the large fruit bat *Eidolon helvum* (Osmaston, 1965). The flesh of *P. excelsa* is fetid. On the Nyika Plateau in Malawi, at the time of year when its kernels form an important item in the diet of the brown-necked parrot (*Poicephalus robustus*), the flesh, which is peeled off the fruits and discarded by the birds, gives forests where it occurs a distinctive odor (Dowsett-Lemaire, pers. comm.).

The fruits of *Parinari curatellifolia* are said to be eaten by elephants, baboons, monkeys, and various kinds of antelope (Palmer & Pitman, 1972), as well as by man. Information on their flavor is somewhat contradictory, possibly because it is difficult to describe. The great explorer David Livingstone, who was buried under a tree of this species, mentions sweetness with the flavor of strawberries and a touch of nauseousness (1857: 237). In Zambia the fallen fruits of *P. curatellifolia* are eaten by the common duiker, *Sylvicapra grimmia* (Wilson, 1966).

Birds have not been recorded eating *Parinari excelsa,* possibly because the flesh is meager in relation to the size of the stone, whereas the green pigeon will take the relatively more fleshy fruits of *P. curatellifolia* (Dowsett-Lemaire, pers. comm.). Both *P. curatellifolia* and *Treron australis* occur in Madagascar, and it is possible that the former was transported across the Mozambique Channel by the latter. Until recently, *Treron* was thought not to play an important part in dispersal because its muscular grinding gizzard was known to destroy the seeds of the wild figs which feature prominently in its diet (Cowles & Goodwin, 1959). However, viable diaspores of four tree species (*Cassine transvaalensis, Croton gratissimus, Diospyros lycioides,* and *Pappea capensis*) have been recovered from the feces beneath the roost of a green pigeon in the Transvaal (Dean, pers. comm.).

DIOSPYROS FERREA

In some parts of its range the fruits of *Diospyros ferrea* show little variation, whereas elsewhere they are quite variable. In different places different vertebrates are available for dispersal and some of the variation appears to be related to this. West of Wallace's Line, both in Asia and Africa, the fruits of *D. ferrea* are relatively uniform. Their dispersal is not known for certain, but the very similar fruits of *D. abyssinica* in Malawi are dispersed by bulbuls and possibly other small birds (Dowsett-Lemaire, pers. comm.). It is perhaps significant that on the African mainland most species of *Diospyros* have fruits dispersed by nonflying mammals (White, unpubl.) and that only *D. abyssinica* and *D. ferrea,* which are thought to be bird-dispersed, oc-

cur on the volcanic island of São Tomé in the Gulf of Guinea (White, 1984). East of Wallace's Line the fruits of *D. ferrea* are quite variable, especially in New Guinea, New Caledonia, and the Fiji–Tonga–Samoa archipelago (Fig. 6).

In the herbarium, the complex variation shown by *Diospyros ferrea* in New Caledonia and Fiji appears to be continuous, and on herbarium evidence alone, the recognition of more than one major taxon would be difficult to justify. In Fiji the largest fruits of *D. ferrea* lie towards the upper limit of those that can be swallowed by fruit pigeons, but whether the pigeons effect dispersal requires confirmation. In New Caledonia the maximum fruit size is smaller than in Fiji.

In New Guinea *Diospyros ferrea* sensu lato is even more variable than elsewhere and it seems likely that certain extreme variants might merit specific rank, although, once again, without fieldwork the relevant criteria are lacking. In Australia (Cribb & Cribb, 1982) the fruits of *D. ferrea* are one of the favorite foods of *Ducula spilorrhoa*, the Torres Strait or Australian pied imperial pigeon, an obligate fruit-eater. Frith (1982) has also seen it take the fruits of *D. ferrea* in the pockets of depauperate rain forest and monsoon forest of the Northern Territory. In Hawaii, fruit pigeons are absent and the fruits of *D. ferrea* are much less variable than in New Guinea and Fiji.

HIRTELLA ZANZIBARICA AND OTHER AFRO-MALAGASY TAXA

In *Hirtella* the fruit is a small drupe. Its relatively thin succulent mesocarp is easily separated from the thin bony endocarp, which on germination splits along 4–7 longitudinal lines of weakness. The fruits of *H. racemosa* are eaten by birds (Macedo, 1977; Macedo & Prance, 1978). In Trinidad the bearded bellbird (*Procnias averano*, Cotingidae) feeds them to its young (Snow, 1970).

The fruit of *Hirtella zanzibarica* on the African mainland is similar to that of the American species, which suggests that it may be dispersed in a similar way. The Malagasy plant, however, has a larger drupe. Its pericarp is much more fibrous and with a less clear distinction between the layers. Lines of weakness are not evident. Its structure is sufficiently different to suggest a different means of dispersal. This requires investigation in the field, but the vertebrate faunas are so different on the two sides of the Mozambique Channel that such an explanation is not improbable.

Virtually nothing is known about the dispersal of fruits by vertebrates in Madagascar beyond the inference that for plant genera also occurring in Africa the situation must usually be different. This is suggested by *Hirtella*. In vegetative characters and in the inflorescence some specimens of *H. zanzibarica* from Africa and Madagascar are barely distinguishable and the flowers differ only slightly. The fruits from Madagascar, however, resemble those of the American genus *Couepia*, said to be dispersed mainly by bats and agoutis, more than they resemble *Hirtella*. Indeed, in a recent monograph of neotropical Chrysobalanaceae (Prance, 1972) the fruits of *H. zanzibarica* from Madagascar would key out to *Couepia*. This example suggests that in crossing a faunal boundary as narrow as the Mozambique Channel, what is otherwise a single species, can, in its fruits, acquire the features of a different genus.

In other Malagasy genera there are similar examples. The populations of *Prunus africana* (Rosaceae) in Africa and Madagascar are thought to be conspecific (Kalkman, 1965), but the fruits in Madagascar are larger and the endocarp is thicker (White, pers. obs.). The genus *Symphonia* (Guttiferae) in particular would repay careful study. *Symphonia globulifera*, the only non-Malagasy species, is widespread in tropical America and Africa. Its fruits are relatively uniform, a large-seeded berry up to 3.5 cm in diameter. By contrast, 16 endemic species of *Symphonia* are recorded from Madagascar (Perrier de la Bâthie, 1951). Their fruits show considerable variation in shape and size. In some species, e.g., *S. eugenioides*, they are smaller (2.5 × 2.2 cm) than in *S. globulifera*, but in *S. macrocarpa* they may attain 20 × 10 cm. Those of *S. fasciculata* can weigh up to one kilogram. Nothing is known of their manner of dispersal. The same is true for the indehiscent, leathery-fleshy fruits of *Humbertioturraea* (Meliaceae). In its floral features it is similar in all respects to typical *Turraea* (Pennington & Styles, 1975), which has capsular fruits and arillate seeds.

Discussion

CRYPTIC EVOLUTION IN THE FRUITS OF VERTEBRATE-DISPERSED PLANTS

In previous sections we have discussed certain vertebrate-dispersed plant genera and species complexes that occur on both sides of major faunal boundaries and have summarized what is

known of their potential dispersers in different parts of their geographical ranges. We have also described variation in the fruits of these and other groups of closely related plants, both allopatric and sympatric, in relation to the animals that are known to disperse them or are thought likely to do so. Much of the variation we have described is cryptic in the sense that little was known about it until it was studied in the field; in other cases its biological significance is still not known.

Cryptic variation in the fruits of vertebrate-dispersed plants may be much more widespread than has previously been supposed, and until it has been detected and carefully described, the taxonomy of the plants themselves will remain largely unresolved and our evolutionary understanding of them will be seriously impaired. In particular, a knowledge of dispersal of fruits by vertebrates may have much to contribute to such questions as the differences in floristic richness in faunistically different parts of the world and to different patterns of speciation in relation to different patterns of vertebrate dispersal.

We are aware of the danger of ignoring extinct vertebrates and the role they might have played as dispersers of extant plant species. We also recognize that it is important to consider the effect the physical environment has had in the diversification of floras, although this may often have been less than has been thought in the past; nevertheless in plants that are both abiotically pollinated and dispersed it must be considerable.

We consider here how geological and especially tectonic events in different parts of the world have resulted in major regional differences in faunas, while regional differences in floras, including floristic richness and patterns of speciation, are examined in the light of these faunal differences. Tectonic history has also contributed to regional floristic differences in other ways, especially by producing regions with different degrees of geological stability.

VERTEBRATE DISPERSAL AND THE IMPROVEMENT OF TAXONOMY

The plant groups we have dealt with have either had a long history of taxonomic confusion or have recently been shown to include more entities than had previously been supposed. The reason for this stems largely from a lack of well-preserved mature fruits and of information, especially on dispersal. In some cases, when this situation was remedied, the taxonomy was found to be simple. This is true for some sympatric species of *Aglaia* in Sundaland and for *Guarea cedrata* and *G. mayombensis* in Africa. In both cases there are important differences in the fruit related to different methods of dispersal. Other instances of "cryptic speciation" which were not finally cleared up until field evidence was available are not difficult to find. A good example would be *Trichilia emetica* and *T. dregeana* (Meliaceae) (White, 1986). These species were persistently confused by herbarium botanists for more than a hundred years, although they are unmistakable in the field. The most important taxonomic differences lie in the architecture of the infructescence, which may be related to dispersal, although precise observations have yet to be made.

There are other situations where the complexity appears to be inherent. An extreme case is the ochlospecies *Diospyros ferrea*, which in the herbarium has not proved amenable to taxonomic analysis. *Diospyros ferrea* sensu lato is probably more variable than any other complex taxon currently referred to under a single binomial. Future fieldwork and experiment might reveal some cryptic speciation in this group but we may still be left with a taxonomically intractable situation. In cases like this, the taxonomy will probably always remain at least partly subjective, however much is known about the plants. Biological understanding is ultimately more important than the precise way in which the facts are slotted into a rigid formal taxonomy, and the former should have priority.

The examples mentioned above occur near the ends of a continuous series. The *Hirtella zanzibarica* group and some species complexes in *Aglaia* appear to occupy an intermediate position.

VERTEBRATE DISPERSERS AND PATTERNS OF SPECIATION

The way in which a vertebrate-dispersed plant species undergoes (or fails to undergo) further speciation after crossing a major faunal boundary may be partly influenced by the interplay of two quite different dispersal situations: 1) the ease with which it can cross the faunal boundary, and 2) its subsequent interactions with potential dispersers on the other side. There is sufficient evidence from *Hirtella zanzibarica* and *Diospyros ferrea* to suggest that this idea would be worth investigating further.

Hirtella zanzibarica sensu lato.

The fruits of the Malagasy populations of *Hirtella zanzibarica* are similar to those of the predominantly mammal-dispersed, closely related American genus *Couepia.* Other species of *Hirtella* as well as the mainland populations of *H. zanzibarica* have smaller fruits of different structure, which are similar to those of some American Hirtellas known to be eaten by small, nonterrestrial birds.

On the African mainland *H. zanzibarica* is widespread but monotypic; in Madagascar its geographical range is much smaller but there are four well-defined geographically replacing subspecies (White, 1976a, 1976b). We do not know what disperses *Hirtella* in Madagascar, but among the few Malagasy fruit-eating vertebrates that are available for this, several are not very mobile. This may be reflected in the different taxonomic situations in *Hirtella* on the two sides of the Mozambique Channel.

Fruit is included in the diet of at least half of the species of lemur in Madagascar. Most lemurs have small territories; in extreme cases no more than 6 ha. The brown lemur (*Lemur fulvus*) has a pattern of geographically replacing subspecies similar to, but more extensive than, that of *Hirtella.* Some Malagasy fruit-eating birds, e.g., species of *Coua,* are also somewhat sedentary. The crested *Coua cristata,* said to be a heavy flier, has four geographical races. There may be a connection between the large amount of local endemism found among Malagasy plants with fleshy fruits and the low vagility of some Malagasy fruit eaters.

The fact that *Hirtella zanzibarica* is probably specifically distinct in Africa and Madagascar and has different kinds of fruit on the two sides of the Mozambique Channel suggests that dispersal across the latter is a relatively rare event. This is supported by the following facts: 1) The very high degree of endemism in the Malagasy flora; apparently it is appreciably higher than in New Guinea. 2) All resident fruit-eating birds in Madagascar, with the possible exception of *Treron australis,* are endemic. 3) We know of no evidence that migratory birds play an important part in transporting diaspores from Africa to Madagascar or in the opposite direction.

Diospyros ferrea sensu lato.

The fact that clear-cut taxa have not been detected in this complex suggests that it is relatively easily dispersed by migratory fruit-eaters across water barriers. It is therefore possible that the resulting gene flow is sufficient to retard or obscure speciation which otherwise could have resulted from adaptation to those more locally distributed potential dispersers available in different parts of the range of *Diospyros ferrea.*

The fruits of *Diospyros ferrea* are known to be eaten by one migratory pigeon (*Ducula spilorrhoa*). Other migratory pigeons are widespread in the tropical Far East. There is also circumstantial evidence that *D. ferrea* may be dispersed by migratory waders or shore birds in parts of the Pacific. We know nothing about the dispersal of the larger-fruited variants of *D. ferrea* in New Guinea and the Fiji–Tonga–Samoa archipelago, but there are several possibilities among sedentary birds, especially fruit pigeons, and, in new Guinea, fruit-eating mammals. These points are discussed in turn.

Wading birds as potential dispersers of Diospyros ferrea. Based on observation of certain migratory breeding birds or shore birds that eat similar fruits, there is circumstantial evidence that *D. ferrea* may be dispersed by them to remote islands in the Pacific. One such bird is the bristle-thighed curlew (*Numenius tahitiensis*) of the family Scolopacidae. *Numenius tahitiensis* breeds in Alaska and migrates in winter through the Pacific to as far south as Tahiti (Munro, 1960: 56; Carlquist, 1967). At least at certain times and in certain localities, the principal food of the bristle-thighed curlew is the fruit of *Canthium odoratum* (Guppy, 1906). The drupes of *C. odoratum* are similar in size to the large-seeded berries of *D. ferrea,* and both species occur in the dry forests of Hawaii. Munro records instances of the bristle-thighed curlew visiting the main Hawaiian Islands since the 1890s and mentions that it sometimes breeds there. According to Olson & James (1982b), this species winters fairly commonly in the Leeward Islands to the west of Hawaii but is much less abundant in the main Hawaiian chain; this may be a fairly recent pattern, "as fossils of this species were found in fair numbers on Molokai and Kauai, and less frequently on Oahu."

Another migratory wader, the killdeer, *Charadrius vociferus* (Charadriidae), also sometimes strays to Hawaii and can retain small seeds in its digestive tract for up to 120 hours before defecating them unharmed (De Vlaming & Proctor, 1968). The larger diaspores of *Celtis laevigata,* which also resemble those of *D. ferrea,* may remain in the killdeer's gizzard for 160 hours before they are regurgitated (Proctor, 1968). Proctor believes that retention times like those he

quotes are long enough to enable dispersal to even the most remote oceanic islands.

The role in seed dispersal of a third shore bird, *Arenaria interpres,* the ruddy turnstone (Scolopacidae), would repay careful investigation. It has a circumpolar breeding range and its migrations extend over nearly all of the Northern Hemisphere and a large part of the Southern. It winters in the Hawaiian archipelago, sometimes in large flocks; 50,000 have been estimated for a single small island (Munro, 1960). Bartsch (1922, quoted by Bent, 1929: 278) was surprised to find it alighting in the tops of bushes of *Scaevola* (Goodeniaceae) on Midway Island to feed on the drupes, which again are about the same size as the berries of *Diospyros ferrea.* "Specimens shot on Sand Island were filled with *Scaevola* berries."

Fruit-eating pigeons and long-distance dispersal of Diospyros ferrea. Some species of *Ducula* and *Ptilinopus* have very small geographical ranges, but others are widespread. The collective range of the species mentioned below extends from India far into the Pacific and suggests how some plant species and species complexes with fleshy fruits may have acquired their extensive distributions.

Ducula spilorrhoa, the Australian pied imperial pigeon, is known to eat the fruits of *Diospyros ferrea.* It is widespread in the rain forest of Australia and occurs throughout New Guinea, to which it migrates annually from Queensland (Crome, 1975). *Ducula bicolor,* the pied imperial pigeon, a parapatric member of the same superspecies as *D. spilorrhoa,* extends from the Andaman Islands eastwards to certain small islands off the west and southwest coasts of New Guinea. *Ducula pacifica,* the Pacific pigeon, is widespread from the islands off the northern coast of New Guinea and the Louisiade Archipelago to Tonga and Samoa; it is known to wander in large flocks from island to island. *Ducula aenea,* the green imperial pigeon, is found in India and Ceylon and eastwards to some small islands situated a short distance beyond Sulawesi. In the opposite direction, *Ptilinopus superbus,* the superb fruit dove, ranges from Australia and the Solomon Islands westwards to Sulawesi. It seems that all the larger islands in Wallacea are occupied by at least one widespread species of fruit pigeon.

Possible dispersers of large-fruited Diospyros ferrea. Among several possible dispersers, only fruit pigeons will be considered here. In New Guinea fruit pigeons are more diverse than anywhere else in the world, and the eight species of *Ptilinopus* and *Ducula* studied by Diamond (1973) in lowland rain forest ranged in weight from 49 grams to 802 grams.

There appears to be a good correlation between a bird's size and its diet, although little precise information is available on the specific composition of the latter. Frith et al. (1976) made a study of the food of nine species of *Ducula* and four species of *Ptilinopus* near Port Moresby, New Guinea. Most of their samples were too small to allow interspecific comparisons of diet, but in *P. magnificus,* the magnificent fruit dove, *P. iozonus,* the orange-bellied fruit dove, and *P. perlatus,* the pink-spotted fruit dove, there was little overlap in preferences for food.

East of New Guinea several species of fruit pigeon are confined to a single island or group of islands. One species of *Ducula* and four species of *Ptilinopus* are known only from Fiji in addition to the tooth-billed pigeon, *Didunculus strigirostris,* which is strictly a ground pigeon. New Caledonia has an endemic species in *Ducula* and *Ptilinopus,* whereas *P. greyii,* Grey's fruit dove, is also shared with the New Hebrides. That some of these pigeons may have played a part in the diversification of *Diospyros ferrea* is suggested by the diet of the New Caledonian pigeon, *Ducula goliath.* The latter is known to eat the fruits of the endemic *Diospyros macrocarpa* (*McKee 26152* in FHO), which is a member of a section of *Diospyros* closely related to that which includes *D. ferrea* (White, in prep.). The fruits of *D. macrocarpa* are up to 5 × 2.5 cm, somewhat larger than the largest known fruits of *D. ferrea.* They are also much larger than the fruits (ca. 1 cm long) of *D. pentamera,* of which *D. macrocarpa* is possibly an insular derivative. *Diospyros pentamera* is confined to Australia, where its fruits are eaten by the Wompoo pigeon, *Ptilinopus magnificus* (Hiern, 1873: 240).

From the facts outlined above, we might infer that if considerable diversification in the fruit of one group of species (the *Diospyros pentamera* group) is related to dispersal by different species of fruit pigeon in different parts of its geographical range, then similar diversification might have occurred in a related group of species (the *D. ferrea* group), although the overall situation in the latter is much more complex and other dispersers are also almost certainly involved.

FAUNAL EXTINCTIONS

In several parts of the world many large mammals became extinct at or near the end of the

Pleistocene (Martin & Klein, 1984). Although the causes of these extinctions remain debatable, man, especially hunting man, is often implicated. Until about 10,000 years ago the Pleistocene mammalian megafauna in North America was comparable in its number of genera to that of Africa at the present time (Janzen & Martin, 1982). More recently there have been vertebrate extinctions in Madagascar, Hawaii, and New Zealand. Several mammals, birds, and giant tortoises became extinct in Madagascar between man's arrival at about 500 A.D. and 1100 A.D. (Dewar, 1984). After the Hawaiian Islands were settled by the Polynesians, possibly as early as 400 A.D., the land bird fauna was reduced by extinction to half its former size (Olson & James, 1982a, 1982b). In New Zealand six genera of very large, wingless, cursorial birds of the family Dinornithidae (moas) have disappeared subsequent to the arrival of the Maoris about 1,000 years ago (Campbell & Lack, 1985).

Fruits and seeds of a wide variety of forest trees have been found in the gizzards of the subfossil moas (Burrows, 1980). Fruit was possibly also eaten by some of the extinct mammals and birds of Madagascar, especially the lemuroids and the two genera of large flightless elephant birds (*Aepyornis* and *Mullerornis*). It is also likely that there were fruit-eaters (e.g., the two large crows) among the 39 extinct bird species recently described by Olson & James from Hawaii. It is, however, usually difficult to interpret the role that extinct vertebrates might have had in the evolution of contemporary vertebrate-dispersed plants, especially when little is known of their diets.

According to Janzen & Martin (1982) "there are prominent members of the lowland forest flora of Costa Rica whose fruit and seed traits can best be explained by viewing them as anachronisms. These traits were moulded through evolutionary interactions with the Pleistocene megafauna (and earlier animals)." The animals they had in mind are gomphotheres (mastodonlike proboscidians), ground sloths, glyptodonts, and extinct relatives of the horse. Janzen & Martin (p. 24) refer to the "tens of millions of years" which have been available "for the evolution of a plant-megafauna dispersal syndrome," and Janzen (1985) believed that a plant, in this case *Spondias mombin*, is "seriously culturally deprived if it abruptly loses a major portion of its disperser coterie with which it has evolved for millions of years."

It is quite likely that the extinct megafauna did formerly disperse some species which still persist in the contemporary Costa Rican flora, but we believe that Janzen & Martin may have underestimated the effectiveness of dispersers in the extant fauna. Elsewhere, Janzen & Wilson (in Janzen, 1983: 438) state that the fruits of *Spondias mombin* are eaten whole by coatis, spider monkeys, and howler monkeys, which defecate the kernels within 1–2 days. The taxonomy of neotropical *Spondias* has until recently been confused. Far from being an anachronism, it seems that the genus may have undergone some recent cryptic speciation (see Croat, 1974; Hladik & Hallé, 1979). Some species of *Spondias*, including *S. mombin*, are dispersed by bats (Greenhall, 1956), and water dispersal of *S. mombin* and other species has been known since before the time of Ridley (1930).

Janzen & Martin (1982) also include *Terminalia catappa* in a list of species growing in the lowland evergreen forest of Corcovado National Park, Costa Rica, which they consider to have most or all of the traits of the megafaunal dispersal syndrome. Although this species is naturalized in many parts of the tropics, including Central America, it is in fact indigenous to the Andaman Islands and adjacent islands and to the Malay Peninsula. It is well known to be dispersed principally by bats and seawater (Ridley, 1930; van der Pijl, 1957). Its fruits have been recovered from the claws of fruit bats caught in mist nets (White, unpubl.).

GEOLOGICAL STABILITY, CLIMATIC CHANGE, AND THE DIVERSITY OF FLORAS

In discussing *Diospyros ferrea* we have suggested that genetic mixing following dispersal across water barriers may be sufficiently frequent to retard or obscure speciation which might otherwise result from an evolutionary response in the fruit to the behavior and nutritional needs of the local fruit-eating fauna.

Examples where isolation does not last long enough to allow complete speciation are not, of course, confined to plants with fleshy fruits. When it arises in response to the physical environment it is most likely to occur in regions of geological instability, such as areas of crustal convergence, where new habitats are constantly being created, or in regions of great physiographic diversity with rapid climatic gradients such as Madagascar. In New Guinea both features occur together. Com-

parisons of floristic richness that do not consider geological history are likely to be misleading, as can be seen from a brief consideration of tropical Africa and the tropical Far East.

Africa, with the exception of the Atlas Mountains in the northwest and the Cape Ranges in the South, consists of a continuous crystalline shield of Pre-Cambrian age. Subsequent to the colonization of Africa by angiosperms, there have been localized marine incursions, repeated cycles of uplift and erosion, local crustal warping and rift faulting, and, particularly during and since the Miocene, some volcanic activity which, with the exception of Ethiopia, was relatively localized. Compared with all other major land masses, Africa has been relatively stable. After its separation from Gondwanaland, contact between Africa and Laurasia has been either brief or intermittent or, more recently, the intermingling of biotas has been restricted by the development of desert barriers. There has been much more intermingling in other parts of the tropics.

Compared with Africa, most of the tropical Far East has been very unstable, especially during the last 15 million years. According to Audley-Charles & Hooijer (1973), in the Late Pleistocene and Holocene downfaulting, involving vertical displacements of at least 3,000 m, occurred between the Outer and Inner Banda Arcs. After the Middle Pleistocene, Timor and the volcanic islands of Flores, Alor, and Wetar have been uplifted by 765 m, 250 m, 700 m, and 820 m, respectively. Johns (1986) has recently given a dramatic and vividly illustrated account of the effects of landslides, volcanic activity, and river meanders in New Guinea. Disturbance on this scale does not occur in Africa. Cyclones also have relatively little effect in Africa compared with New Guinea and other parts of the Far East.

Much of the tropical Far East is a gigantic archipelago, but one in which the number and size of the islands and the width of the water barriers have been constantly changing in response to changing sea levels throughout the Quaternary, especially on the continental shelves. This must have provided many opportunities both for speciation and the breakdown of incipient speciation, and has greatly influenced the total species richness of this region.

A region of physiographic diversity like New Guinea, besides providing a wide range of contemporary habitats, might influence species richness indirectly by providing refugia during times of climatic instability. In places where the climatic gradients are steep, a small shift in range may be sufficient for a species to escape extinction. In Africa the Zambezian region, though broadly similar in climate to the Sudanian region, is floristically much richer (White, 1965). This might be explained at least in part because the greater physiographic diversity of the former has provided more opportunities for speciation (White, 1976c) in the past but also for survival during the Quaternary changes in climate.

There are some indications that taxonomically intractable complexes such as *Diospyros ferrea* are more plentiful in the Far East than in Africa, possibly for the reasons we have discussed above. Workers familiar with the variability of Far Eastern species sometimes express surprise when they make comparisons with African species (Ng, pers. comm.; Pennington, pers. comm.). Thoroughly analyzed Far Eastern ochlospecies include *Vavaea amicorum* (Pennington, 1969) and the *Diospyros sylvatica, hermaphroditica, fasciculosa* species complex (Ng, 1971). *Diospyros ferrea* behaves as an ochlospecies both in Africa and the Far East, but it is much more variable in the latter. Nevertheless, by African standards it is very variable. In more than 30 years White has found few other African species which match the African populations of *D. ferrea* in complexity.

LACK OF INFORMATION: HOW PROGRESS MIGHT BE ACHIEVED

In the foregoing account we have stressed the lack of well-preserved fruits and the almost total absence of detailed observations on the dispersal of fruits by vertebrates. Here we make a few suggestions for future progress.

It is essential that fieldworkers should attempt to collect fruits at all stages of development and especially when they are fully ripe; they should be preserved in spirit or some other preserving fluid. Herbarium curators should be prepared to provide permanent storage space for this material. Full descriptions of features not readily seen in preserved specimens are necessary, preferably supplemented by sketches, photographs, and, where appropriate, colored drawings.

There is a need for greater cooperation between plant taxonomists and workers in other fields, especially those zoologists, primatologists, and biochemists who are interested in the interactions between fruits and their dispersers. It would be helpful if botanists were more willing to identify and retain the voucher specimens col-

lected by such workers. This material is often incomplete or poorly preserved, and it is more likely to be welcomed by botanists if those who collect it try to obtain good specimens and to preserve them when fresh. For imperfect material and in groups which have not been recently revised, botanists can sometimes only provide provisional or incomplete names. Nevertheless, it is useful if the voucher specimens are cited in the specialist literature. The work of Rijksen (1978) on the ecology of the orangutan, *Pongo pygmaeus*, is supported by herbarium collections. By examining his specimens and visiting his study area, Pannell was able to incorporate his observations on *Pongo pygmaeus* and *Aglaia* into her own publication (Pannell & Koziol, 1987).

Floras and monographs are more interesting to read and more generally useful when their authors have studied (not merely collected) the living plant. This is usually possible only to a limited extent. Hence the value of collaboration between botanists and other biologists, whether amateur or professional. Our own work has greatly benefited from information provided by friends and colleagues in other disciplines.

Where morphological information on fruits does exist, it would be valuable for this to be included in botanical illustrations. Until now, ripe fruits have rarely been depicted, and detail of seeds and endocarps has often been lacking. If future illustrations were to include such information, identification of diaspores recovered from animal feces or intestines might become easier, and this would lead to more information on seed dispersal by animals.

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PHYTOGEOGRAPHY OF THE ALEXANDRIA FOREST (SOUTHEASTERN CAPE PROVINCE)

P. B. PHILLIPSON AND S. RUSSELL[1]

ABSTRACT

The Alexandria Forest lies near the coast in the extreme southeast corner of Africa, in a region where five major phytochoria meet and which has recently been recognized as an important "tension zone" with respect to plant evolution and migration in southern Africa. Despite its potential interest to phytogeographers and taxonomists, the forest has previously received minimal attention. A checklist of woody taxa occurring in the forest was compiled and the occurrence of each taxon in forests of other regions of southern Africa was determined. Distribution patterns for each species were compared and classified with the assistance of a standard computer data-sorting program. A total of 167 taxa were recorded, 17 of which were common to all forest regions, and 8 of which have been recorded only in the Alexandria Forest. The forest has floristic affinities with other forests in southern Africa, particularly the neighboring coastal forests to the west and to the northeast, and to the inland montane forests of the Eastern Cape Province, with which it shares between 56% and 69% of its taxa. However, the analysis confirms that the Alexandria Forest is phytogeographically distinct from forests in other regions, and its position as a significant floristic link between the forests of the Afromontane and Indian Ocean Coastal Belt phytochoria is demonstrated.

RÉSUMÉ

La forêt d'Alexandrie est située près de la côte dans l'extrême sud-est de l'Afrique, dans une région où cinq types de végétation se rencontrent et qui a été récemment reconnue comme une zone importante de "tension" concernant l'évolution et la migration dans le sud de l'Afrique. Malgré l'interêt potentiel qu'elle peut avoir pour les phytogéographes et les taxonomistes, la forêt a recu peu d'attention. Une liste des espèces ligneuses de la forêt a été dressée et on a déterminé la présence de chaque taxon dans les forêts d'autres régions du sud de l'Afrique. Des shémas de répartition pour chaque espèce ont été comparés et classés à l'aide d'un programme informatisé. On a enregistré un total de 167 taxons, dont 17 se trouvaient dans toutes les régions de forêt et dont 8 n'apparaissaient que dans la forêt d'Alexandrie. Cette forêt a des affinités floristiques avec d'autres forôts du sud de l'Afrique, en particulier les forêts côtières avoisinantes vers l'ouest et le nord-est et les forêts de montagne de l'intérieur à l'est de la Province du Cap où l'on retrouve de 56 à 69% de ses taxons. Cependant, l'étude confirme que la forêt d'Alexandrie est distincte des forêts dans d'autres régions d'un point de vue phytogéographique et les auteurs démontrent sa position comme un lien floristique important entre les forêts aframontanes et celles de la ceinture côtière de l'océan Indien.

The Alexandria Forest consists of patches of indigenous forest occurring in the Eastern Cape Province of South Africa, between Humansdorp (34°02′S, 24°45′E) and the mouth of the Keiskamma River (33°17′S, 27°28′E). Of these patches, the Langebos near the town of Alexandria is the largest and best preserved. The climax forest has been replaced by secondary grassland or thorn scrub throughout much of the Alexandria Forest veld type (sensu Acocks, 1975), which covers approximately 3,000 km² (Fig. 1). Long recognized as a valuable timber resource, especially of boxwood (*Buxus macowanii*), the Alexandria Forest Reserve formed one of the largest forest management units in the Cape at the beginning of this century (Sim, 1907). Although often mentioned in the forestry literature (Brown, 1887; Phillips, 1931; King, 1941), very little botanical work has yet been carried out on the forest.

The Alexandria Forest occupies an interesting phytogeographical position, occurring in an area where five major African phytochoria converge. These are the Indian Ocean Coastal Belt (Tongaland–Pondoland Regional Mosaic), the Sudano–Zambesian Region, the Afromontane Region, the Karoo–Namib Region, and Capensis (Werger, 1978). Various phytochorological boundaries have been drawn in the neighborhood of the Alexandria Forest since the time of Drège (1844) (see maps in Marloth, 1908; Werger, 1978). Doubt remains as to whether the forest has closer affinities with the southern Cape coastal forests (e.g., Knysna), the east coast forests to the north, or the inland forests of the Eastern Cape. Acocks classified all the coastal

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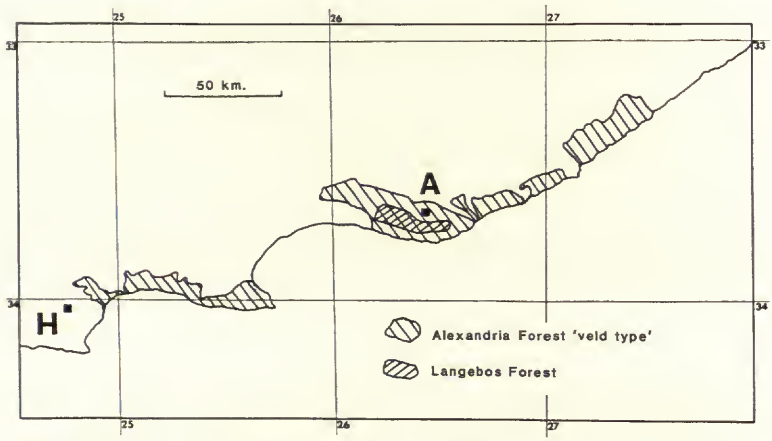


FIGURE 1. Map showing the distribution of the Alexandria Forest veld type, which contains patches of indigenous forest (e.g., Langebos). The towns marked are Humansdorp (H) and Alexandria (A).

forests in South Africa as "Coastal Tropical Forest," while noncoastal forests were classified either as "Inland Tropical Forest" or "Inland Temperate and Transitional Forest and Scrub" according to their latitude. White (1978) considers that the southern Cape forests belong with these inland forests as the southernmost 'island' of the Afromontane archipelago which, at lower latitudes, occurs further from the coast and at higher altitudes. In the same biogeographic classification, the Alexandria Forest is included with the coastal forests to the north as part of the Indian Ocean Coastal Belt, although its strong Afromontane affinities are recognized (Moll & White, 1978). In a primarily ecological study, Marker & Russell (1984) mention the similarity of the Alexandria Forest to certain communities in the inland montane forests of the eastern Cape.

White (1983) has commented that "little has been published on the transition from Afromontane forest to lowland communities." This, coupled with the paucity of botanical data on the Alexandria Forest and the uncertainty of its floristic affinities, prompted the compilation of a full list of woody plants for the forest. The distribution of these taxa in other southern African forests was analyzed and a method developed to numerically assess the phytogeographic affinities of the Alexandria Forest flora.

METHODS

SPECIES LIST: ALEXANDRIA FOREST

Only woody plants (trees, shrubs, and woody climbers) have been included in the present study, since their taxonomy is better understood and their distribution generally better known than for the majority of herbaceous taxa. Information was drawn from Schönland (1919), Dyer (1937), Martin & Noel (1960), Palmer & Pitman (1972), Acocks (1975), Coates Palgrave (1977), and Marker & Russell (1984). Unpublished data was obtained from R. A. Lubke and from the field notebooks of J. P. H. Acocks, loaned by courtesy of the Botanical Research Institute, Pretoria. Each record was thoroughly checked against distribution data in relevant floras (Harvey & Sonder, 1859–1865; Thiselton-Dyer, 1896–1933; Codd et al., 1963–) and taxonomic monographs (where available), which also provided some additional records. No record was accepted unless its occurrence in the Alexandria Forest region in a forest habitat was specifically mentioned and unless it agreed with generalized distribution data. This rigorous approach necessitated the omission of certain previously published records, which may have been the result of misidentifications made in the field.

DELIMITATION OF FOREST REGIONS IN SOUTHERN AFRICA

Southern African forests can be divided into seven regional groups on the basis of their occurrence in the Afromontane and Indian Ocean Coastal Belt phytochoria, and on distributional discontinuities within each phytochorion (Fig. 2). These groups correspond closely with the forest veld types of Acocks (1975) and with specific forest localities discussed by White (1978) and

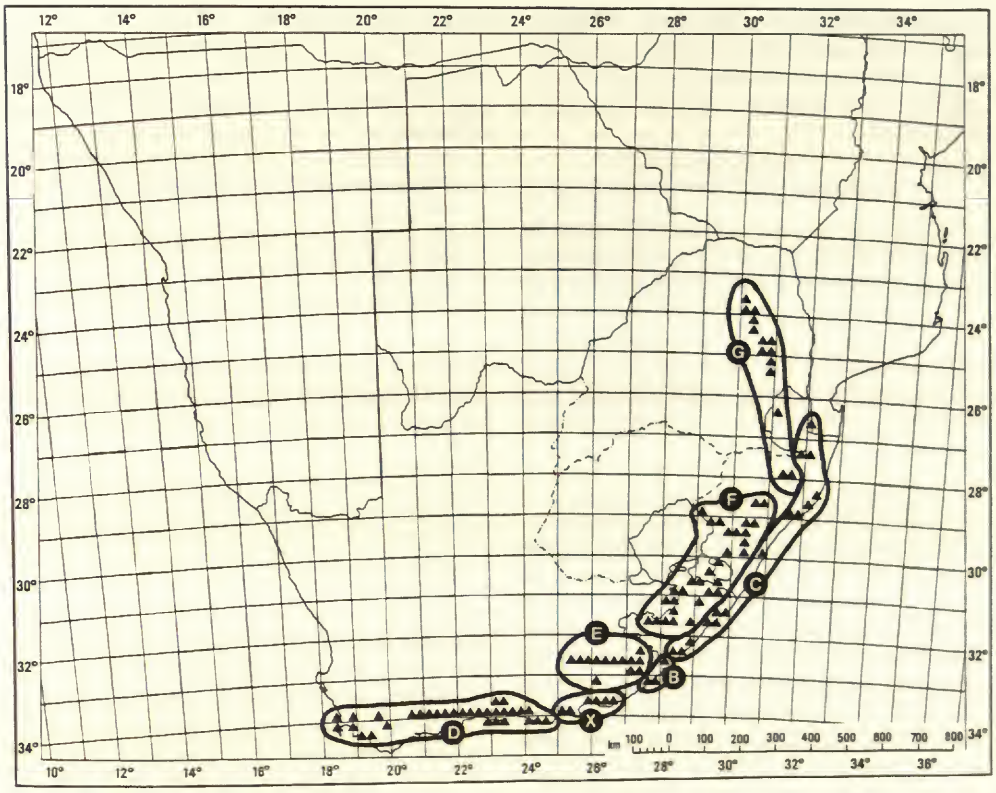


FIGURE 2. Distribution of forests in southern Africa mapped by ¼ degree squares. The forests form seven regional groups:—A. Alexandria.—B. Eastern Cape Coastal.—C. Transkei and Natal Coastal.—D. Southern Cape.—E. Eastern Cape Montane.—F. Transkei and Natal Montane.—G. Transvaal. N.B. To avoid confusion, coastal forests occurring in specialized habitats, including dune forest, are omitted from this map.

Moll & White (1978). Forests of limited extent also occur in certain specialized habitats within the Indian Ocean Coastal Belt and tend to have a distinctive and specialized flora. Forests of these habitats have been omitted from the present study, except for those on littoral sand dunes. The dune forest is floristically related to typical coastal forest in southern Africa (Moll, 1978). It occurs in suitable habitats along the east and south coasts but with only isolated, depauperate patches west of Port Elizabeth (Moll & White, 1978). In this analysis, dune forest is treated as an additional forest region. Species recorded from the Alexandria Forest were scored for their occurrence in the other seven forest regions of southern Africa. The sources of data already mentioned were consulted, and additional sources for each forest region are as follows: A. *Dune Forest*. Henkel et al. (1936), Comins (1962), Edwards (1967), Moll (1972), Rogers & Moll (1975), Venter (1976). B. *Eastern Cape Coastal Forest* (occurring between the Kei and Keiskamma rivers). Comins (1962), C. Vernon (unpubl. data for the Fort Grey Forest Reserve). C. *Transkei and Natal Coastal Forest* (including forest in the Lebombo Mountains). Henkel et al. (1936), Huntley (1965), Edwards (1967), Rogers & Moll (1975), Moll (1977). D. *Southern Cape Forest*. Phillips (1931), Von Breitenbach (1974), McKenzie (1978). E. *Eastern Cape Montane Forest* (south of the Kei River, primarily on the Winterberg range; Amatole Mountains, Katberg, Boschberg, etc.). Story (1952), Comins (1962), Phillipson (unpubl. data for the Amatole Mountains). F. *Transkei and Natal Montane Forest* (excluding those north of 28°S). West (1949), Killick (1958, 1962), Taylor (1963), Moll & Haigh (1966), Edwards (1967), Moll (1968). G. *Transvaal Forest* (including Ceza and Ngome Forests in Natal, and forest of the Swaziland highveld).

Van der Schijff & Schoonraad (1971). The same rigorous approach to the acceptance of records was taken as described for the Alexandria Forest, and certain previously published records had to be excluded.

COMPUTER ANALYSIS OF DATA

The data obtained were prepared for computer analysis by giving each taxon a seven-character code representing its presence or absence in each of the seven forest regions. This distribution code enabled rapid sorting of the taxa into groups with particular distributional characteristics, using a standard sorting program. The groups were then compared on the basis of various distributional parameters.

COEFFICIENT OF CHOROLOGICAL AFFINITY

The results obtained by computer analysis were expected to provide information of value in assessing the chorological affinities of the flora of the Alexandria Forest. Clearly those taxa that are common to all or most forest regions are less significant floristic links than those with more restricted distributions. On the other hand, the total number of taxa shared between two regions is also significant. A method was therefore developed that provides in a single coefficient a synthesis of these two aspects. This method is treated in two parts.

1. In this analysis, the Alexandria Forest is referred to as the "primary region" and the other forest regions as "secondary regions." Taxa common to Alexandria and the first secondary region were divided into seven groups according to the number of secondary regions from which they have been recorded. The first group contains taxa that have only been recorded from Alexandria and the first secondary region, while the last contains taxa that have been recorded from all regions.

2. Each group was weighted by dividing its number of taxa [$G(n)$] by its number of secondary regions (n). Thus the first group is weighted by the factor 1, the second group by the factor ½, and so on. A total of these weighted group values was calculated and is referred to as the distribution value (DV) for a particular forest region in relation to Alexandria. Distribution values were calculated for the remaining forest regions following the same procedure. A similar value was then calculated for Alexandria itself by dividing the whole data set into seven groups. This is referred to as the total distribution value (TDV). The coefficient (C) for each secondary region was then calculated by dividing DV for that region by TDV. This can be written in general terms as follows:

$$DV \text{ (for each secondary region)} = \sum_{n=1}^{x} G(n)/n;$$

$$TDV = \sum_{n=1}^{x} T(n)/n;$$

$$C \text{ (for each region)} = DV \text{ (for that region)}/TDV;$$

where x = total number of secondary forest regions in study and $T(n)$ = total number of taxa common to primary region and n secondary regions.

RESULTS

SPECIES LIST

The species list for the Alexandria Forest consists of 167 woody taxa, of which 136 (81.4%) are trees (sensu Coates Palgrave, 1977) (Appendix 1 with distributional data). In some cases distinction of infraspecific taxa was possible. However, for convenience, the term species will be used in presenting and discussing the results.

DISTRIBUTION ANALYSIS

The following seventeen species (10.2%) are common to all forest regions: *Apodytes dimidiata* subsp. *dimidiata, Canthium inerme, Canthium obovatum, Carissa bispinosa, Cassine tetragona, Dovyalis rhamnoides, Ekebergia capensis, Ficus sur, Grewia occidentalis, Hippobromus pauciflorus, Chionanthus foveolata, Ochna arborea* var. *arborea, Olea capensis* subsp. *macrocarpa, Psychotria capensis, Scolopia zeyheri, Scutia myrtina,* and *Zanthoxylum capense.*

The following thirteen species (7.8%) are common to all forest regions, except the ecologically-specialized dune forest: *Calodrendrum capense, Cissampelos torulosa, Clausena anisata, Curtisia dentata, Diospyros whyteana, Maytenus peduncularis, Nuxia floribunda, Pittosporum viridiflorum, Podocarpus falcatus, Podocarpus latifolius, Rapanea melanophloeos, Rhus lucida,* and *Scolopia mundii.*

The number of species common to Alexandria Forest and each other forest region is given in Table 1.

The following eight species (4.8%) are recorded only from Alexandria Forest: *Aloe speciosa, Ata-*

TABLE 1. Number of species common to Alexandria and each other forest region.

Forest Region	Number of Taxa
T'kei and Natal Coastal	115 (68.9%)
Eastern Cape Coastal	114 (68.3%)
Eastern Cape Montane	103 (61.7%)
Southern Cape	95 (56.9%)
T'kei and Natal Montane	83 (49.7%)
Dune	77 (46.1%)
Transvaal	72 (43.1%)

laya capensis, Brachylaena ilicifolia, Cotyledon velutina, Nylandtia spinosa, Phyllanthus heterophyllus, Smelophyllum capense, and *Sterculia alexandri.*

Nineteen species (11.4%) are recorded only from Alexandria Forest and one other forest region; these are listed in Table 2. The frequency of the most common patterns is given in Table 3.

TABLE 2. Numbers of species only found in Alexandria and one other region.

Forest Region	Number of Species	Species List
Southern Cape	8	*Cassine peragua* *Clutia daphnoides* *Cynanchum obtusifolium* var. *obtusifolium* *Euclea racemosa* *Lachnostylis hirta* *Rhus laevigata* *Sparrmannia africana* *Virgilia divaricata*
Eastern Cape Coastal	4	*Ehretia rigida* *Euphorbia triangularis* *Pavonia praemorsa* *Protasparagus oxyacanthus*
Dune	3	*Rhoiacarpos capensis* *Rhus incisa* var. *effusa* *Turraea obtusifolia*
Eastern Cape Montane	2	*Croton rivularis* *Microglossa mespilifolia*
T'kei and Natal Montane	1	*Senecio brachypodus*
Transvaal	1	*Solanum geniculatum*
T'kei and Natal Coastal	0	—

TABLE 3. Most common forest distribution patterns of Alexandria Forest flora, with numbers of species.

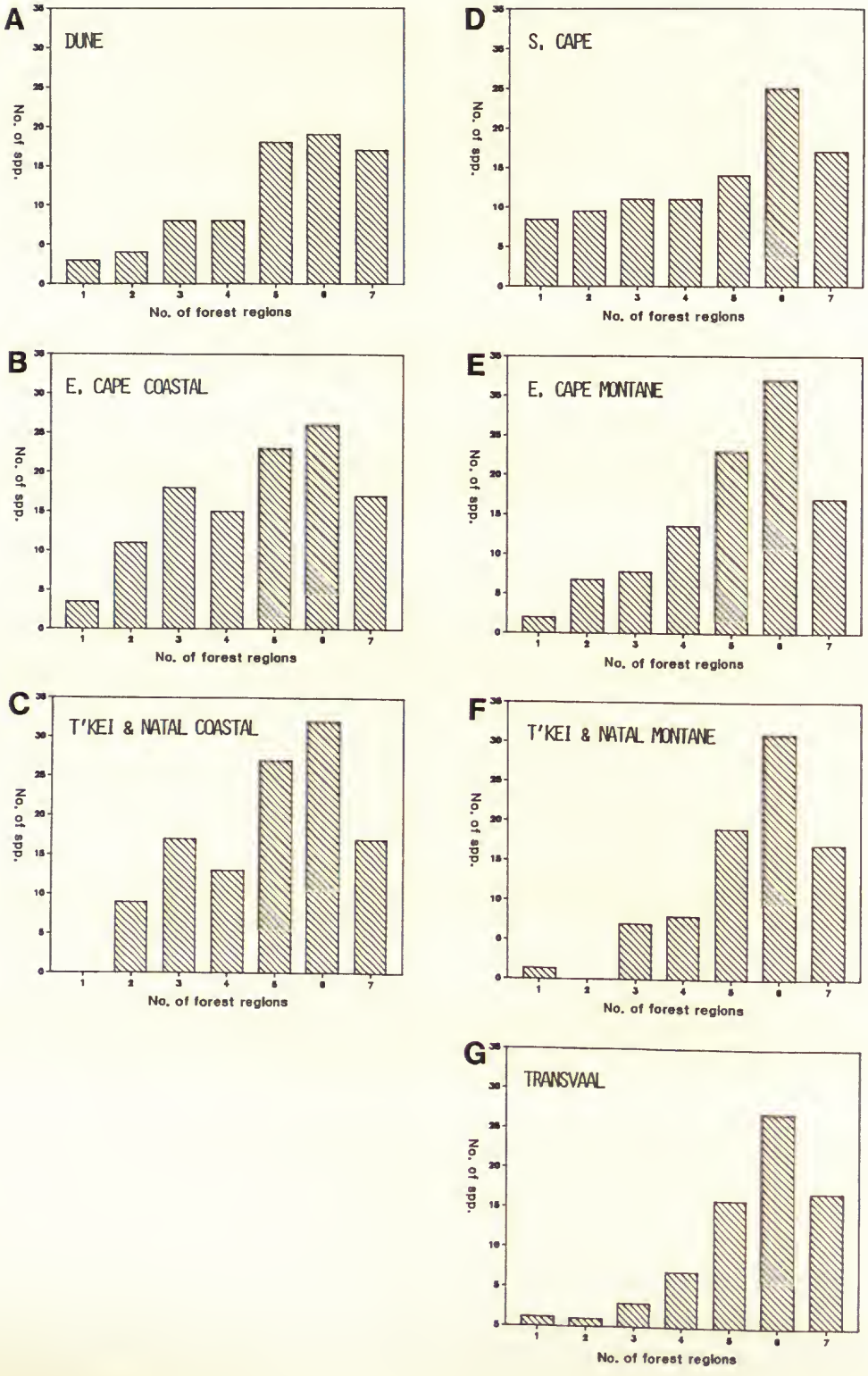
Distribution Pattern	Number of Species
All forest regions	17
All except Dune	13
Only Alexandria	8
Only Alexandria and Southern Cape	8
All except Southern Cape	7
All except Eastern Cape Coastal	6
All except Southern Cape and Transvaal	6
All except Transvaal	5
Only Alexandria, Dune and Eastern Cape Coastal	5

A graphical representation of the groups that were formed in the process of calculating the coefficient is given as a series of bar diagrams (Fig. 3). In these diagrams each bar represents one group. The overall shape of the diagrams indicates the relative numbers of species with restricted and widespread distributions shared between Alexandria Forest and each of the secondary forest regions. A diagram that ascends steeply from left to right corresponds to a low number of restricted species and a high number of widespread species.

The coefficient of chorological affinity for each forest region in relation to the Alexandria Forest is given in Table 4.

DISCUSSION

Many authors have commented on the high species richness of southern African forests. The Alexandria Forest conforms well to this generalization, with 167 woody species. It has a similar number of species to the larger southern Cape forests (Phillips, 1931) and Eastern Cape montane forests (Phillipson, unpubl. data). Many of the species recorded from the Alexandria Forest are more or less ubiquitous in southern African forests. Some of these species are also widespread in forests in tropical Africa, either in the Afromontane Region (e.g., *Apodytes dimidiata* subsp. *dimidiata, Calodendrum capense*) or in the Indian Ocean Coastal Belt (e.g., *Sideroxylon inerme, Vepris lanceolata*), or in both (e.g., *Scolopia zeyheri, Scutia myrtina*). Despite such species, the Alexandria Forest has a distinct flora. This is demonstrated by the relatively low numbers of


A
DUNE
No. of spp.
No. of forest regions
B
E. CAPE COASTAL
No. of spp.
No. of forest regions
C
T'KEI & NATAL COASTAL
No. of spp.
No. of forest regions
D
S. CAPE
No. of spp.
No. of forest regions
E
E. CAPE MONTANE
No. of spp.
No. of forest regions
F
T'KEI & NATAL MONTANE
No. of spp.
No. of forest regions
G
TRANSVAAL
No. of spp.
No. of forest regions

species shared with neighboring forest regions (43–69%) and by the high number of species with restricted distribution. Nineteen species (11%) are recorded in only one other forest region, and eight (4.8%) have been recorded only from the Alexandria Forest. Of these apparent endemics, five are marginal in forest habitats. They are more typically plants of drier habitats and have various phytochorological affinities. The remaining three species (*Atalaya capensis, Smelophyllum capense,* and *Sterculia alexandri*) are essentially endemic to the Alexandria Forest.

Previous work has suggested a link between the Alexandria Forest and the floristically richer coastal forests further north. In terms of total number of species in common, the present study confirms this conclusion (Table 1). However, a close relationship with the southern Cape forests also exists. This is demonstrated by the high number of species restricted to these two regions (Table 2). Similarity of the Alexandria Forest to the three inland forests is less pronounced. These three regions show remarkably consistent patterns of affinity with Alexandria, which decrease with distance (Fig. 3E–G). The numbers of solely Afromontane species and Indian Ocean Coastal Belt species recorded from Alexandria Forest are very similar (27 and 26, respectively). Individual species could be chosen to indicate the forest's Afromontane affinity (e.g., *Myrsine africana*) or its coastal affinity (e.g., *Acokanthera oblongifolia*). The present study suggests that the placement of the Alexandria Forest with either phytochorion is an arbitrary choice when based on presence of woody species.

The existence of an important Cape component in southern African forests was accepted by early phytogeographers. Many included at least the southern Cape forests in the Cape region (e.g., Bolus, 1905). Results of the present study appear to give support to this opinion. The number of solely Cape Province species present is higher (35 species) than the equivalent values for the Afromontane and Indian Ocean Coastal Belt phytochoria. However, like the apparent endemics mentioned earlier, these species are mainly marginal in forest habitats. They are also mainly widespread species typical of drier habitats (e.g., *Buddleja saligna, Rhus undulata, Schotia afra*) and do not constitute a distinct "Cape" forest flora. The penetration of such species into the Alexandria Forest is interesting and confirms the close relationship of the Forest to drier vegetation types, as suggested by Acocks (1975).

TABLE 4. Coefficient of phytochorological affinity of seven forest regions to the Alexandria Forest.

Forest Region	Coefficient
Eastern Cape Coastal	0.56
Southern Cape	0.52
T'kei and Natal Coastal	0.48
Eastern Cape Montane	0.44
Dune	0.34
T'kei and Natal Montane	0.30
Transvaal	0.27

Recent work has discussed the phytogeographic complexity of the Eastern Cape, which has been termed a "tension zone" between the relevant phytochoria (Gibbs Russell & Robinson, 1981; Cowling, 1983). The present study confirms this complexity, and it must be concluded that the distinction between the Afromontane and Indian Ocean Coastal Belt phytochoria breaks down to a large extent in southeast Africa. Moll & White (1978) give examples of forests that contain intermediate communities occurring as far north as Natal.

The coefficient described in this paper provides an effective and repeatable means of phytochorological comparison, and the results obtained are consistent with the conclusions of previous authors. The coefficients highlight the close relationship of the Alexandria Forest to the Eastern Cape coastal forest. Ecological methods and the clustering techniques used in numerical taxonomy may be adapted for phytogeographic purposes (see Peters, 1971, for a review, and Clayton & Hepper, 1974, for an example). Such methods require a complete data set for each region, which would be a much greater undertaking than the present study. Numerical methods have not been used widely by plant geographers, possibly because of the difficulty in

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FIGURE 3. Bar diagrams representing the number of species common to Alexandria Forest and other forest regions.—A. Dune.—B. Eastern Cape Coastal.—C. Transkei and Natal Coastal.—D. Southern Cape.—E. Eastern Cape Montane.—F. Transkei and Natal Montane.—G. Transvaal. For each region the species are divided into seven groups, each represented by a bar, according to the number of (secondary) forest regions in which they occur.

obtaining the large amount of data necessary. A simple coefficient such as described above may have a useful general application in phytochorological studies.

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Appendix I.

Species list for the Alexandria Forest, with distribution data. Species also recorded from the following forest regions:—A. Dune.—B. Eastern Cape Coastal.—C. T'kei and Natal Coastal.—D. Southern Cape.—E. Eastern Cape Montane.—F. T'kei and Natal Montane.—G. Transvaal. * indicates infraspecific taxon uncertain.

Acokanthera oblongifolia (Hochst.) Codd	ABC
A. oppositifolia (Lam.) Codd	ABCDEF
Allophyllus decipiens (Sond.) Radlk.	BDE
A. natalensis (Sond.) De Winter	ABCF
Aloe speciosa Bak.	—
Apodytes dimidiata E. Mey. ex Arn. subsp. *dimidiata*	ABCDEFG
Atalaya capensis R. A. Dyer	—
Azima tetracantha Lam.	BEF
Behnia reticulata (Thunb.) Didr.	ABCEFG
Brachylaena discolor DC.*	ABCG
B. glabra (L. f.) Druce	CD
B. ilicifolia (Lam.) Phill. & Schweick.	—
Buddleja dysophylla (Benth.) Radlk.	CEF
B. saligna Willd.	DE
Buxus macowanii Oliv.	BC
Calodendrum capense (L. f.) Thunb.	BCDEFG
Calpurnia aurea (Ait.) Benth. subsp. *sylvatica* (Burch.) Brummitt	BCEF
Canthium ciliatum (Klotzsch) Kuntze	ABCEFG
C. inerme (L. f.) Kuntze	ABCDEFG
C. mundianum Cham. & Schlechtd.	ACDEFG
C. obovatum Klotzsch	ABCDEFG
C. spinosum (Klotzsch) Kuntze	DFG
Capparis fascicularis DC. var. *fascicularis*	BCEG
C. fascicularis DC. var. *zeyheri* (Turcz.) Toelken	BC
C. sepiaria L. var. *citrifolia* (Lam.) Toelken	ABCDE
Carissa bispinosa (L.) Desf. ex Brenan*	ABCDEFG
C. aethiopica Thunb.	ABCDF
C. crocea (Thunb.) Kuntze	BD
C. peragua L.	D
C. tetragona (L. f.) Loes.	ABCDEFG
Celtis africana Burm. f.	ACDEFG
Chaetacme aristata Planch.	ABCEF
Chionanthus foveolata (E. Mey.) Stearn	ABCDEFG
Chrysanthemoides monilifera (L.) T. Norl.*	ABCDEF
Cissampelos torulosa E. Mey. ex Harv.	BCDEFG
Clausena anisata (Willd.) Hook. f. ex Benth.	BCDEFG
Clematis brachiata Thunb.	ABCEFG
Clerodendrum glabrum E. Mey. var. *glabrum*	ABCFG
Clutia daphnoides Lam.	D
C. pulchella L. var. *pulchella*	CDEF
Cordia caffra Sond.	ABC
Cotyledon velutina Hook. f.	—
Crotalaria capensis Jacq.	BDFG
Croton rivularis Muell.-Arg.	E
Curtisia dentata (Burm. f.) C. A. Sm.	BCDEFG
Cussonia spicata Thunb.	BCEFG
C. thyrsiflora Thunb.	ABD
Cynanchum ellipticum (Harv.) R. A. Dyer	ABDE
C. obtusifolium L. f. var. *obtusifolium*	D
Cyphostemma cirrhosum (Thunb.) Desc. ex Wild & Drum. subsp. *cirrhosum*	AE
Diospyros dichlorophylla (Gand.) De Winter	BCD
D. villosa (L.) De Winter var. *villosa*	ABCE
D. whyteana (Hiern) F. White	BCDEFG
Dombeya tiliacea (Endl.) Planch.	BCF
Dovyalis lucida Sim	ACEFG
D. rhamnoides (Burch. ex DC.) Harv.	ABCDEFG
Dracaena hookeriana K. Koch	ABCEFG
Ehretia rigida (Thunb.) Druce	B
Ekebergia capensis Sparrm.	ABCDEFG
Embelia ruminata (E. Mey. ex A. DC.) Mez	ACEF
Encephalartos altensteinii Lehm.	BCE
Erythrina caffra Thunb.	ABCDE
Euclea crispa (Thunb.) Guerke var. *crispa*	CDEFG
E. natalensis A. DC.*	ABCEF
E. racemosa Murray	D
E. schimperi (A. DC.) Dandy*	ABCDEG
E. undulata Thunb. var. *undulata*	BD
Eugenia zeyheri Harv.	ABCEF
Euphorbia triangularis Desf.	B
Ficus burtt-davyi Hutch.	ABCDE
F. sur Forssk.	ABCDEFG
F. thonningii Bl.	CG
Gardenia amoena Sims	BCEFG
G. thunbergia L. f.	ABCEF
Gonioma kamassi E. Mey	BCD
Grewia occidentalis L.	ABCDEFG
Harpephyllum caffrum Bernh.	ABCEF
Hippobromus pauciflorus (L. f.) Radlk.	ABCDEFG
Homalium rufescens Benth.	BC
Jasminum angulare Vahl	BCE
Kiggelaria africana L.	CDEFG
Lachnostylis hirta (L. f.) Meull. Arg.	D
Maerua cafra (DC.) Pax	ABCDG
M. racemulosa (DC.) Gilg & Ben.	ABCDEF
Maytenus heterophylla (Eckl. & Zeyh.) N. K. B. Robson	ABCDEF
M. mossambicensis (Klotzsch) Blakelock var. *mossambicensis*	ABCEF
M. nemorosa (Eckl. & Zeyh.) Marais	ACDE
M. peduncularis (Sond.) Loes.	BCDEFG
M. procumbens (L. f.) Loes.	ACD
M. undata (Thunb.) Blakelock	ABCEFG
Microglossa mespilifolia (Less.) B. L. Robinson	E
Mimusops obovata Sond.	ABCEFG
Myrsine africana L.	DEFG
Nuxia congesta R. Br. ex Fresen.	BCG
N. floribunda Benth.	BCDEFG
Nylandtia spinosa (L.) Dumort.	—
Ochna arborea Burch. ex DC. var. *arborea*	ABCDEFG
O. serrulata (Hochst.) Walp.	CDEFG
Olea capensis L. subsp. *macrocarpa* (C. H. Wr.) Verdoorn	ABCDEFG
O. capensis L. subsp. *capensis*	BCDE
O. europaea L. subsp. *africana* (Mill.) P. S. Green	BDEG
O. exasperata Jacq.	ABC
O. woodiana Knobl.	ABCFG

Olinia ventosa (L.) Cufod.	BDF
Pavetta lanceolata Eckl.	BCEFG
P. revoluta Hochst.	ABC
Pavonia praemorsa (L. f.) Cav.	B
Phyllanthus heterophyllus E. Mey.	–
Pittosporum viridiflorum Sims	BCDEFG
Pleurostylia capensis (Turcz.) Oliv.	BCEF
Plumbago auriculata Lam.	BE
Podocarpus falcatus (Thunb.) R. Br. ex Mirb.	BCDEFG
P. latifolius (Thunb.) R. Br. ex Mirb.	BCDEFG
Protasparagus africanus (Lam.) Oberm.	BCDEG
P. densiflorus (Kunth) Oberm.	AC
P. oxyacanthus (Bak.) Oberm.	B
P. racemosus (Willd.) Oberm.	ABCDG
P. setaceus (Kunth) Oberm.	ACDEFG
P. suaveolens (Burch.) Oberm.	BC
P. subulatus (Thunb.) Oberm.	BCG
Psychotria capensis (Eckl.) Vatke	ABCDEFG
Ptaeroxylon obliquum (Thunb.) Radlk.	BCEFG
Pterocelastrus tricuspidatus (Lam.) Sond.	ABDE
Pupalia atropurpurea Moq.	AC
Putterlickia pyracantha (L.) Szyszyl.	AB
Rapanea melanophloeos (L.) Mez	BCDEFG
Rhamnus prinoides L'Herit.	CDEFG
Rhoiacarpos capensis (Harv.) DC.	A
Rhoicissus digitata (L. f.) Gilg & Brandt	ABDEF
R. tomentosa (Lam.) Wild & Drum.	ACDEFG
R. tridentata (L. f.) Wild & Drum.	ACDEFG
Rhus incisa L. f. var. *effusa* (Presl) R. Fernandes	A
R. laevigata L.	D
R. longispina Eckl. & Zeyh.	BD
R. lucida L.	BCDEFG
R. refracta Eckl. & Zeyh.	DE
R. undulata Jacq. var. *undulata*	DE
Sarcostemma viminale (L.) R. Br.	BD
Schotia afra (L.) Thunb. var. *afra*	BDE
S. latifolia Jacq.	BDEG
Scolopia mundii (Eckl. & Zeyh.) Warb.	BCDEFG
S. zeyheri (Nees) Harv.	ABCDEFG
Scutia myrtina (Burm. f.) Kurz	ABCDEFG
Secamone alpini Schultes	ACDEFG
S. filiformis (L. f.) J. H. Ross	ABCEFG
Senecio brachypodus DC.	F
Sideroxylon inerme L.	ABCDE
Smelophyllum capense Radlk.	–
Solanum geniculatum E. Mey.	G
S. giganteum Jacq.	DEF
Sparrmannia africana L. f.	D
Sterculia alexandri Harv.	–
Strychnos decussata (Pappe) Gilg	ACD
S. spinosa Lam	BCF
Suregada africana (Sond.) Kuntze	ACE
Syzygium cordatum Hochst.	BCFG
Tarchonanthus camphoratus L.	ABCD
Teclea natalensis (Sond.) Engl.	ABCEG
Tecomaria capensis (Thunb.) Spach.	BC
Trichocladus crinitus (Thunb.) Pers	BCD
T. ellipticus Eckl. & Zeyh. ex Walp.	DE
Turraea obtusifolia Hochst.	A
Vepris lanceolata (Lam.) G. Don	ABCDEF
Virgilia divaricata Adamson	D
Viscum obscurum Thunb.	BCDE
V. rotundifolium L. f.	BCDEG
Zanthoxylum capense (Thunb.) Harv.	ABCDEFG

DISTRIBUTION DES TYPES DE VÉGÉTATION ET CLIMAT: QUELQUES RÉSULTATS STATISTIQUES RELATIFS AU ZAÏRE

T. RICHEL[1]

RÉSUMÉ

La méthode des profils écologiques, mise au point par une équipe de chercheurs français dans un but principalement phytosociologique, a été appliquée à l'étude de la distribution de la végétation au Zaïre. Le comportement de cinq types de végétation face à 27 paramètres climatiques a été comparé. Entre forêts claires et forêts denses sèches, une différence est apparue, qui semble indiquer une préférence du second type pour les zones à climat plus contrasté. Pour ce qui est des variables, leur efficacité à rendre compte de la répartition observée est analysée. Parmi les paramètres étudiés, le plus efficace est le type de climat de Köppen; la durée de la saison sèche n'est pas prépondérante, pas plus que les variables liées à la pluviosité ou celles indiquant des valeurs extrêmes. Les paramètres nettement intercorrélés se sont avérés plus efficaces que les variables "isolées."

ABSTRACT

The method of ecological profiles, developed by a team of French researchers with a primarily phytosociological goal, was applied to the study of vegetational distribution in Zaire. The behavior of five types of vegetation with respect to 27 climatic parameters was compared. Open forests and dry dense forests differ, which suggests a preference by the latter for zones with more contrasting climates. The usefulness of the variables to explain the observed distribution is analyzed. Among the parameters studied, the most useful is the Köppen climate type; the length of the dry season is not preponderant, no more so than the variables associated with precipitation or those indicating extreme values. The clearly intercorrelated variables were more useful than the "isolated" variables.

On sait que la distribution de la végétation est sous l'influence de multiples facteurs de l'environnement et on considère généralement que c'est le climat qui exerce l'action globale la plus importante (Good, 1964; Walter, 1979).

En zone tempérée, de nombreux travaux ont mis en évidence des relations entre climat et distribution de la végétation, on a par ailleurs constaté que des corrélations observées sous des latitudes moyennes ne se retrouvaient pas en zone intertropicale (Mather & Yoshioka, 1966).

Pour ce qui concerne l'Afrique intertropicale, malgré l'existence d'études détaillées d'écophysiologie et de micrométéorologie (par exemple, Monteith, 1975–1976) et de synthèses à l'échelle mondiale (Walter, 1979), on ne trouve guère de travaux récents portant sur ce type de problème à une échelle régionale.

Le but de cette contribution est de comparer globalement le comportement de différent types de végétation face à une série de paramètres climatiques dont il s'agira également d'évaluer l'impact individuel; certaines hypothèses concernant la prépondérance d'un ou de plusieurs facteurs (la durée de la saison sèche, par exemple) seront testées.

La récente publication de la carte de végétation d'Afrique (White, 1983), celle plus ancienne de la végétation du Zaïre (Devred, 1958), et l'existence de nombreuses observations climatologiques cartographiées au Zaïre (Bultot, 1971–1974) constituent la base indispensable à ce travail.

MÉTHODE

RÉCOLTE DES DONNÉES

Le territoire zaïrois a été divisé en 839 carrés d'un-demi degré de côté. Cette grille superposée à la carte de végétation et aux différentes cartes climatiques a permis d'associer chaque carré à une unité cartographique d'une part, et à une série de valeurs de paramètres climatiques préalablement regroupés en différentes classes d'autre part. Toutes les unités cartographiques impliquant la présence d'un même type de végétation ont été envisagés simultanément; on a obtenu ainsi les présences totales suivantes:

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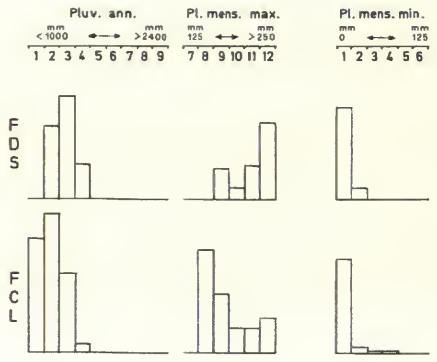

PROFILS INDICES — PLUVIO MENS MAX

	7	8	9	10	11	12
FORET DENSE OMBROPHILE	-	---	--	0	+++	0
FORET DENSE SECHE	E	E	0	---	0	+++
FORET CLAIRE	E	+++	++	0	-	0
SAVANE BOISEE OU ARBUSTIVE	E	0	0	++	0	--
SAVANE HERBEUSE	E	++	+	--	0	0

FIGURE 1. Exemples de profils écologiques des fréquences corrigées et de profils "indicés." +, ++, +++ = présence significativement supérieure à la valeur attendue. −, −−, −−− = présence significativement inférieure à la valeur attendue. Le nombre de signes indique le seuil: respectivement 5, 1 et 0.1%. 0 = présence non significativement différente de la valeur attendue. E = échantillon trop petit pour tirer une conclusion.

Forêt dense ombrophile (FDO)	629
Forêt dense sèche (FDS)	50
Forêt claire (FCl)	156
Savane boisée et arborée (Sb)	222
Savane herbeuse (Sh)	42

TRAITEMENT DES DONNÉES

Les techniques d'étude des profils écologiques, mises au point par des chercheurs de Montpellier, ont été utilisées. Daget & Godron (1982) en donnent une description détaillée; nous en résumerons les phases essentielles.

Il est utile de rappeler ici qu'une liaison statistique n'implique nullement un quelconque rapport de cause à effet entre les variables envisagées; aussi, en accord avec les auteurs cités, parlerons-nous de descripteurs plutôt que de facteurs écologiques.

Les formules données dans le texte font appel aux conventions suivantes:

NK: nombre de classes d'un descripteur.
NR: nombre de relevés (carrés) total.
R(K): nombre de relevés dans la classe K.
U(K): nombre de présences dans la classe K.
V(K): nombre d'absences dans la classe K.
U(E): nombre total de présences.
V(E): nombre total d'absences.

Le profil écologique des fréquences corrigées d'un type de végétation en fonction d'un descripteur est établi en calculant, pour chaque classe, l'indice:

$$\frac{U(K)}{R(K)} \cdot \frac{NR}{U(E)}.$$

La signification statistique de ce type de profil peut être révélée par un test exact conduisant à établir un profil "indicé" (Gauthier et al., 1977), où les valeurs sont remplacées par un indicateur de signification: + (−) pour une liaison positive (négative), le nombre de signes étant lié au seuil (5, 1 ou 0.1%), "0" indique une espèce non significativement sensible et "E" signifie que l'échantillon est trop faible pour autoriser une conclusion.

L'information mutuelle entre un type de végétation et un descripteur est calculée par

$$I(L;E) = \sum_{1}^{NK} \frac{U(K)}{NR} \log_2 \frac{U(K)}{R(K)} \cdot \frac{NR}{U(E)} + \sum_{1}^{NK} \frac{V(K)}{NR} \log_2 \frac{V(K)}{R(K)} \cdot \frac{NR}{V(E)}$$

(Guillerm, 1971). Elle sera d'autant plus haute que la présence d'un type de végétation dépendra de la variable écologique. Il faut cependant tenir compte de l'échantillonnage, par l'intermédiaire du calcul de l'entropie facteur

$$H(L) = \sum_{1}^{NK} \frac{R(K)}{NR} \log_2 \frac{NR}{R(K)}$$

(Guillerm, 1971). L'efficacité globale d'un descripteur par rapport à un type de végétation est donnée par le rapport entre information mutuelle et entropie facteur. C'est la valeur qui servira de base à nos comparaisons car elle peut indiquer l'efficacité du descripteur à "expliquer" la distribution du type de végétation (Lepart & Debussche, 1980). Par ailleurs, les descripteurs utilisés sont plus ou moins liés les uns aux autres, certains tests impliquant leur indépendance, il était important de mesurer leurs corrélations, nous les avons calculées grâce au rapport de corrélation qui indique l'intensité de la liaison entre deux séries de valeurs quelle que soit la forme de la relation les unissant (Dagnelie, 1973). Nous avons présenté certains résultats sous forme de dendrogrammes obtenus par la méthode d'enchaînement simple (Dagnelie, 1975).

TABLEAU 1. Efficacité des descripteurs, en pourcent.[1]

	Variable	FDO	FDS	FCl	Sb	Sh	Moyen
1	Climat de Köppen[2]	19.31	3.24	14.97	11.26	3.52	10.46
	Pluviosité annuelle						
2	Min. en 40 ans	15.75	2.27	13.78	5.69	1.91	7.88
3	Min. en 10 ans	15.98	2.24	13.01	4.81	3.18	7.84
4	Max. en 40 ans	17.14	2.67	15.10	7.90	2.62	9.09
5	Max. en 10 ans	17.05	2.72	15.35	7.88	2.72	9.14
6	Moyenne	17.06	2.93	15.41	6.53	2.59	8.90
	Pluviosité mensuelle						
7	Max. moyen (+)	3.56	1.03	1.66	0.97	1.10	1.66
8	Min. moyen	12.97	3.56	12.64	6.68	3.45	7.86
9	Durée de la saison sèche	12.99	3.55	11.92	7.04	3.62	7.82
	Déficit de saturation moyen						
10	Mensuel max.	11.24	3.03	11.94	4.81	2.68	6.74
11	Mensuel min. (+)	0.57	0.07	0.03	8.14	0.14	1.79
12	Annuel	12.50	4.44	12.27	4.21	3.78	7.44
	Rapport pluviosité/déficit de saturation moyen[3]						
13	Mensuel max. (+)	6.91	1.60	5.02	2.91	1.75	3.64
14	Mensuel min. (+)	11.30	3.89	11.15	7.69	3.20	7.33
15	Annuel	6.74	1.42	7.33	7.86	2.02	5.07
	Moyenne des données de pluviosité	11.55	2.54	10.47	5.94	2.48	6.60
	Température						
16	Moyenne	19.93	2.62	11.95	3.42	1.66	7.92
17	Min. absolue[4]	15.85	3.31	11.66	4.17	2.13	7.42
18	Max. absolue[4] (+)	10.70	1.49	7.42	4.77	1.14	5.10
	Température journalière minimum moyenne						
19	Annuelle	20.39	3.27	12.45	1.73	2.84	8.14
20	Mois le plus froid	20.90	3.78	13.17	6.18	2.35	9.28
21	Mois le plus chaud	20.72	3.76	14.76	5.30	3.13	9.53
	Température journalière maximum moyenne						
22	Annuelle	24.07	2.96	17.58	1.75	3.41	9.95
23	Mois le plus froid (+)	18.45	2.08	13.12	1.36	1.14	7.23
24	Mois le plus chaud (+)	5.76	0.32	1.73	4.61	2.04	2.89
	Amplitude thermique journalière moyenne						
25	Annuelle	13.05	3.85	11.15	3.22	2.24	6.70
26	Mensuellle max.	11.53	3.92	11.38	5.57	2.82	7.04
27	Mensuelle min. (+)	1.27	0.13	0.95	1.20	0.25	0.76
	Moyenne des données de température	15.22	2.62	10.61	3.61	2.10	6.83
28	Type de sol[5]	5.53	2.39	5.03	1.89	0.60	3.09

[1] Sauf indication contraire, les données sont tirées de l'ouvrage de Bultot, 1971–1974.
[2] Bultot, 1950
[3] Rapport de Meyer (in Daubenmire, 1967).
[4] Vandenplas, 1947.
[5] FAO/UNESCO, 1976.

RÉSULTATS ET DISCUSSION

COMPORTEMENT DE LA VÉGÉTATION FACE À CERTAINS DESCRIPTEURS

La Figure 1 présente quelques profils des fréquences corrigées et profils indicés. De manière générale, on peut constater que, des conditions les plus humides vers les plus sèches, on voit logiquement se succéder forêt dense ombrophile, savane boisée et arborée, forêt dense sèche, forêt claire, et savane herbeuse.

Le type savane boisée et arborée, et dans une

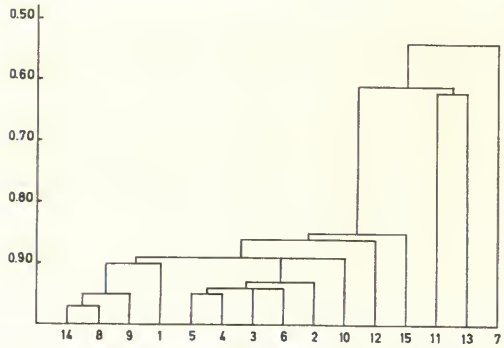

FIGURE 2. Classification des descripteurs liés à la pluviosité et au type de climat; la numérotation est celle du Tableau 1. On a porté en ordonnée la valeur du rapport de corrélation.

moindre mesure les savanes herbeuses, présentent parfois un profil bi-modal, probablement en rapport avec l'hétérogénéité de ces végétations au point de vue de leur origine par exemple. Généralement, les préférences des forêts claires et des forêts denses sèches sont très proches, une intéressante exception à cette règle se présente dans le cas des pluviosités mensuelles maximales. La forêt dense sèche est liée préférentiellement à des pluviosités mensuelles maximales nettement plus élevées que la forêt claire, face aux pluviosités mensuelles minimales et à la durée de la saison sèche, ces deux types de végétation se comportent cependant de manière similaire. On peut donc constater que, par rapport à la forêt claire, les forêts denses sèches du Zaïre occupent des zones à contraste plus marqué entre saison sèche et humide. La controverse autour des rapports de ces deux types de végétation (par exemple, White, 1983; Lebrun & Gilbert, 1954) rend d'autant plus intéressante cette différence de préférence climatique. Bien entendu, cette conclusion demande à être vérifiée dans un cadre géographique plus large que le Zaïre. Il faut d'autre part également remarquer que l'efficacité du descripteur "type de sol" est relativement plus importante pour les forêts denses sèches.

EFFICACITÉ DES DESCRIPTEURS

Les valeurs de l'efficacité de chaque descripteur par rapport aux cinq types de végétation sont indiquées dans le Tableau 1. On peut constater que le type de climat de Köppen est moyennement le plus efficace; il s'agit d'un descripteur composé où interviennent température, pluviosité et durée de la saison sèche (sensu Bultot, 1950). Remarquons que celle-ci, tout en montrant une efficacité supérieure à la moyenne, n'est pas nettement prépondérante.

A titre de comparaison, nous avons indiqué les valeurs pour le type de sol (sur base de la Carte des sols d'Afrique, publiée par l'UNESCO en 1976), le caractère secondaire de ce descripteur par rapport au climat, prévisible à cette échelle (Lepart & Debussche, 1980), s'observe clairement.

Un examen des corrélations inter-descripteurs (Fig. 2) permet de distinguer globalement une majorité de paramètres fortement corrélés et une minorité de variables plus ou moins isolées. Dans tous les cas, les descripteurs appartenant à un groupe se sont avérés moyennement plus efficaces, ce qui peut résulter d'un effet de renforcement mutuel de différents facteurs réellement actifs.

Une comparaison entre les descripteurs liés au facteur eau et au facteur chaleur ne révèle pas de différence claire entre les deux groupes, rien ici ne va donc dans le sens d'une dominance des facteurs hydriques (Schnell, 1976), on peut même remarquer qu'en dehors du type de climat de Köppen, les plus efficaces sont des descripteurs liés à la température.

Quant aux efficacités des paramètres extrêmes pluri-annuels et moyens, on peut comparer entre elles celles des pluviosités annuelles et des températures, une fois de plus il n'apparaît pas de différence marquée. Notons cependant que les pluviosités annuelles moyennes et extrêmes sont fortement corrélées (rapp. de corr. >0.9), ce qui peut masquer les liens existant entre la végétation et ces descripteurs (Greig Smith, 1964), il est donc délicat de tirer une conclusion. Toutefois, le sens des variations est dépendant des types de végétations envisagés, il n'y a donc pas de différence systématique observable.

COMPORTEMENT GLOBAL DES TYPES DE VÉGÉTATIONS FACE À L'ENSEMBLE DES DESCRIPTEURS

Le nombre de présences total a une forte influence sur la valeur de l'information mutuelle (Bottlikova et al., 1976) et donc sur celle de l'efficacité, par conséquent, seules des valeurs se rapportant à des types de végétation également présentes sont comparables entre elles. Une mesure de corrélation permet cependant de comparer le comportement global des différents types de végétation et de savoir si l'efficacité relative des

TABLEAU 2. Coéfficient de corrélation de rang de Spearman entre les différents types de végétation. Valeurs critiques aux seuils de signification 5%, 1%, et 0.1%: 0.6190, 0.8095 et 0.9286.

	FDS	FCl	Sb	Sh
FDO	0.9048	1.000	0.0476	0.6964
FDS		0.9048	0.1190	0.6845
FCl			0.0476	0.6964
Sb				0.2083

descripteurs est semblable pour les cinq types de végétation. Pour ce faire, nous avons utilisé les huit descripteurs les moins inter-corrélés (marqués d'une "+" au Tableau 1); pour pouvoir tester la signification des résultats sans émettre d'hypothèse quant à la forme des populations, nous avons employé le coéfficient de corrélation de rang de Spearman (Dagnelie, 1973; Lee & Lee, 1982).

Les résultats (Tableau 2) indiquent qu'au seuil de 1%, les types de végétation forestiers présentent le même comportement global, celui des savanes herbeuses s'en distingue légèrement (la corrélation est significative au seuil de 5%), et les savanes boisées se comportent très différemment: le minimum de déficit de saturation jouant un rôle très nettement plus important.

CONCLUSIONS

La méthode utilisée présente certaines difficultés, notamment lorsqu'il faut comparer des échantillons d'effectifs très différents, néanmoins il nous paraît qu'elle est appropriée à des études de distributions.

Il serait sans doute intéressant d'étendre ce genre de traitement à une échelle géographique plus vaste, ce qui demande des données climatiques malheureusement rarement disponibles. D'autre part, nous n'avons envisagé ici que des types de végétation, la même méthode adaptée et appliquée aux distributions spécifiques pourra certainement apporter des éléments nouveaux quant à leur interprétation, notamment concernant l'importance des facteurs écologiques.

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THE TAXONOMY OF *DOMBEYA BURGESSIAE* COMPLEX (STERCULIACEAE) IN AFRICA[1]

J. H. SEYANI[2]

ABSTRACT

Character variation in the *Dombeya burgessiae* complex in Africa was analyzed using field populations, herbarium specimens, and greenhouse plants. The analysis of 23 characters represented by 93 character states shows that variation in the characters is poorly correlated both among the characters and with geography. The variation is kaleidoscopic, and similar phenotypes can occur in widely separate localities. The pattern of variation throughout the geographic range of the species was too poorly structured to justify the recognition of more than 12 taxa. Over 20 binomials previously recognized as separate species are placed in synonymy under *D. burgessiae*. The relationship between *D. burgessiae* and other species of subgenus *Dombeya* are briefly discussed. The species is closely related to *D. buettneri*.

RÉSUMÉ

La variation des caractéristiques du complexe de *Dombeya burgessiae* en Afrique a été analysée à l'aide de populations naturelles, d'échantillons d'herbier, et de plantes de serres. L'analyse de 23 traits représentés par 93 états de caractères montre que les variations dans les caractéristiques sont peu en corrélation à la fois parmi les caractéristiques et avec la géographie. Il est apparu que la variation est kaleidoscopique et que des phénotypes similaires peuvent être trouvés dans des localités très éloignées les unes des autres. Le shéma de variation dans la répartition des espèces est trop peu structuré pour pouvoir justifier la reconnaissance de plus de 12 taxons. Plus de 20 binomiaux qui étaient auparavant reconnus comme des espèces séparées sont mis en synonymie sous *D. burgessiae*. L'auteur discute brièvement les rapports entre *D. burgessiae* et d'autres espèces dans le sous-genre *Dombeya*. L'espèce est très proche de *D. buettneri*.

Dombeya burgessiae Gerr. ex Harv. of subgenus *Dombeya* (*Dombeya* Cav.-Sterculiaceae) is a shrubby species of moist savanna woodlands and margins of montane forests in tropical Africa. In the course of a taxonomic study of the African species of *Dombeya*, I found that this species was one of the most variable in Africa, perhaps equaling that of the *Cryptosepalum exfoliatum* and *C. maraviense* groups (Duvigneaud & Brenan, 1966) or the *Clematopsis scabiosifolia* aggregate (Exell et al., 1951).

Since its publication in 1862 by Harvey, *Dombeya burgessiae* has been a base from which conspecific variants (populations) have been contrasted and/or described as new species by various workers, as evidenced by the accounts of Schumann (1900) and Wild (1961), and by other floristic treatments in the distributional area of the group. This practice, coupled with the great polymorphism of this taxon, has created problems of identification that make the use of keys and visual specimen matching difficult to separate *D. burgessiae* from 'species' such as *D. antunesii, burttii, dawei, greenwayi, calantha, johnstonii, lasiostylis, nyasica, pulchra, sparmannioides, sphaerantha, tanganyikensis, trichoclada,* etc. This problem led Wild (1965) to suggest the application of experimental taxonomic techniques to *D. burgessiae* as one way of understanding the baffling variation. In recent years, the accumulation and availability of good quality herbarium specimens from various regions in Africa have indicated that *D. burgessiae* and its variants (or species of other authors) form what I regard as a complex. Hence, the aim of this investigation was to analyze and define characters in the complex and delimit taxa if any.

METHODS

The variation of morphological characters within the *Dombeya burgessiae* complex was studied using field populations, herbarium material, and greenhouse living collections. The fieldwork was conducted in Malawi, where vegetative (habit, indumentum, leaf shape, stipule shape, etc.) and floral (floral bud shape, inflorescence type, flower color, etc.) characters of many

[1] I am grateful to Mr. F. White for his supervision during my Ph.D. research work at Oxford University, of which this publication is part.

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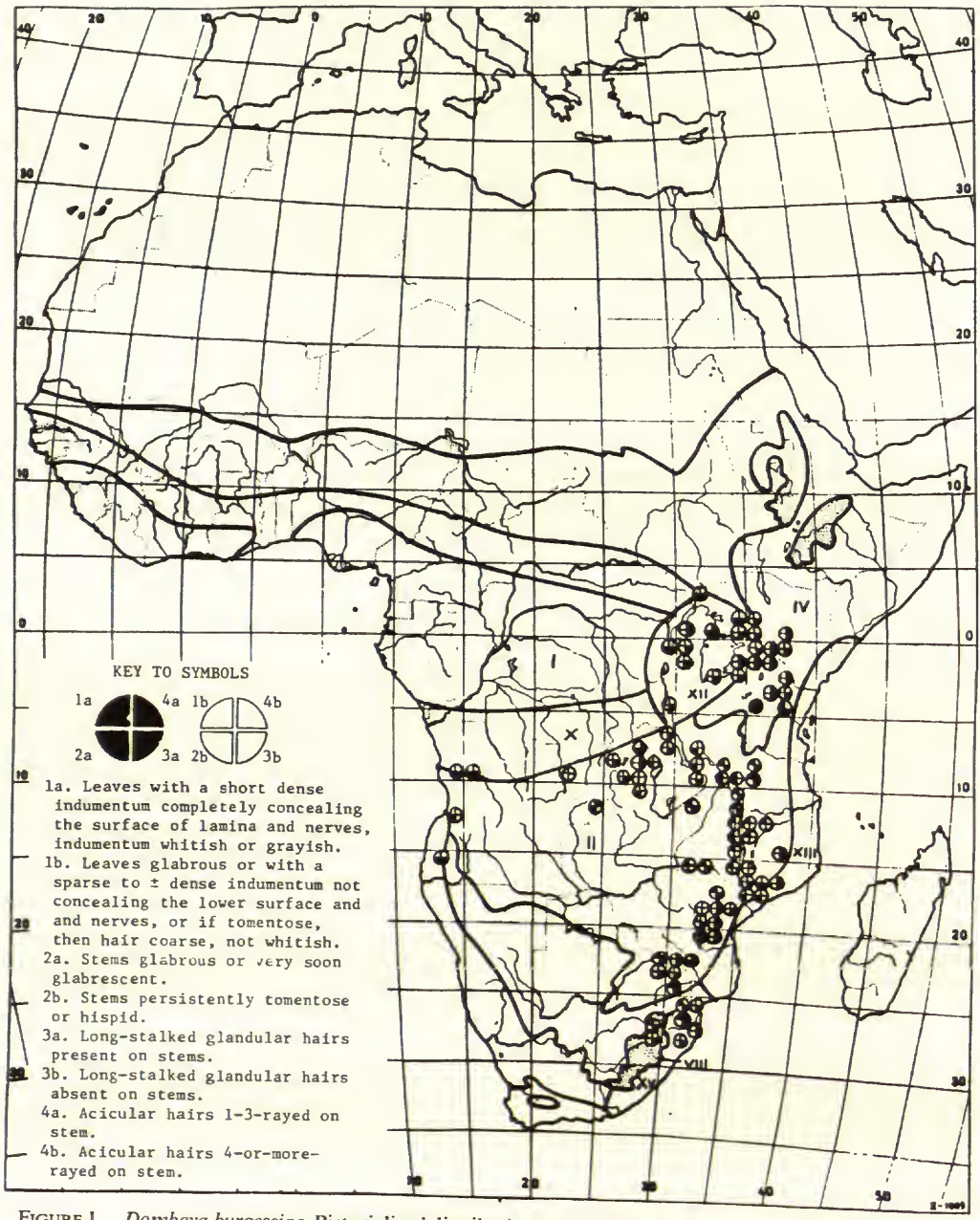

FIGURE 1. *Dombeya burgessiae*. Pictorialized distribution map showing variation in four indumentum characters. (The phytogeographic regions of southern Africa, I–XV, after White, 1983).

populations were recorded. Herbarium voucher specimens of the provenances studied are placed in FHO, K, and MAL (abbreviations follow Holmgren et al., 1981). Mature seeds of 35 populations were collected and used in the greenhouse growth experiments.

The herbarium studies were based on material at BM, BR, CGE, E, FHO, K, MAL, and OXF, and a selection from B, GH, FHI, FI, LISC, P, UPS, and W. The specimens were placed into groups according to their localities (Anonymous, 1969) based on a degree square system (Edwards

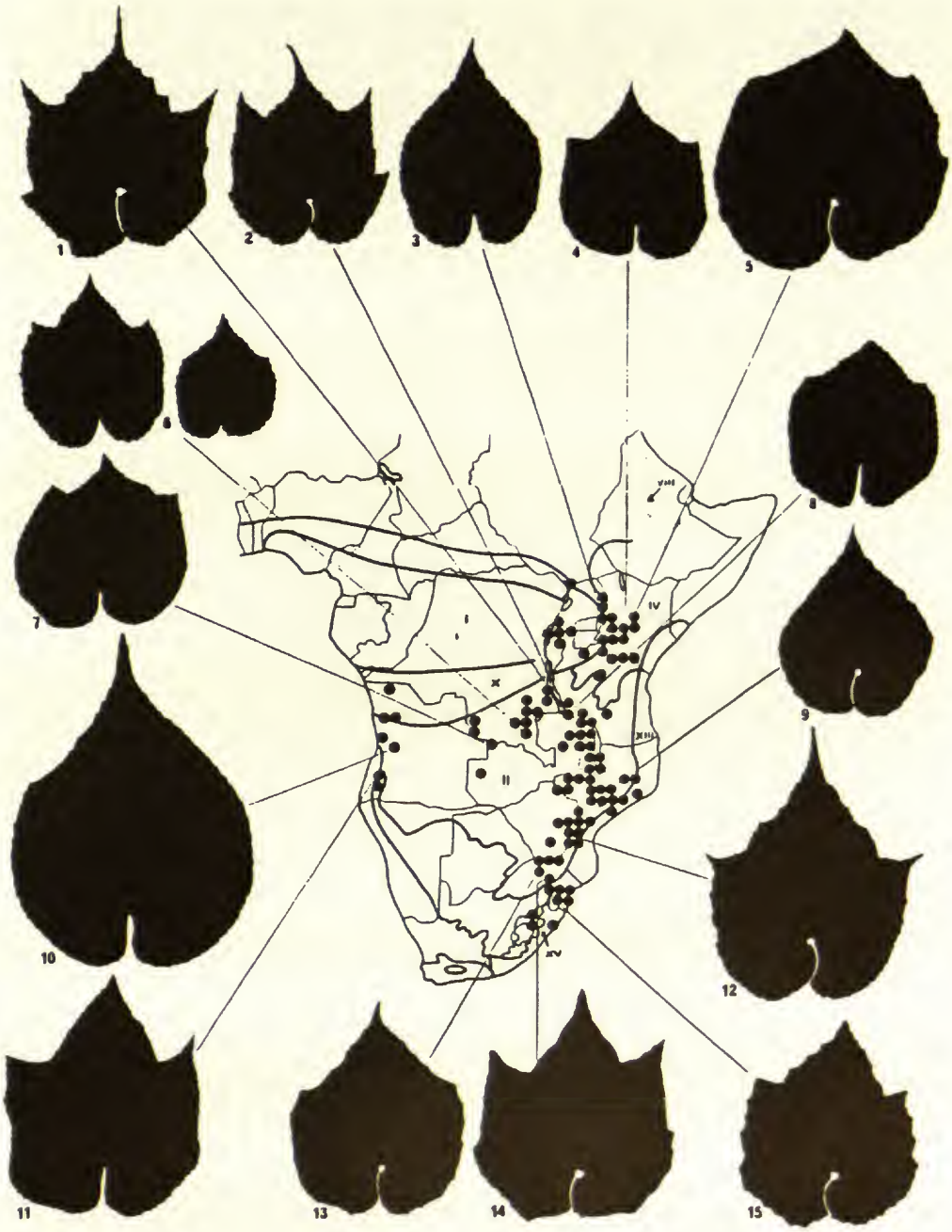

FIGURE 2. Geographical distribution of *Dombeya burgessiae* showing variation in leaf shape.

& Leistner, 1971). These were later subjected to detailed character analysis: leaf shape, leaf color, stipule shape and size, quality and quantity of indumentum, inflorescence type, flower color (as recorded on specimen labels), flower size, number of seeds/locule, locules hairy-glabrous, etc. This analysis resulted in the tabulation of variation in 23 characters distributed in 93 character

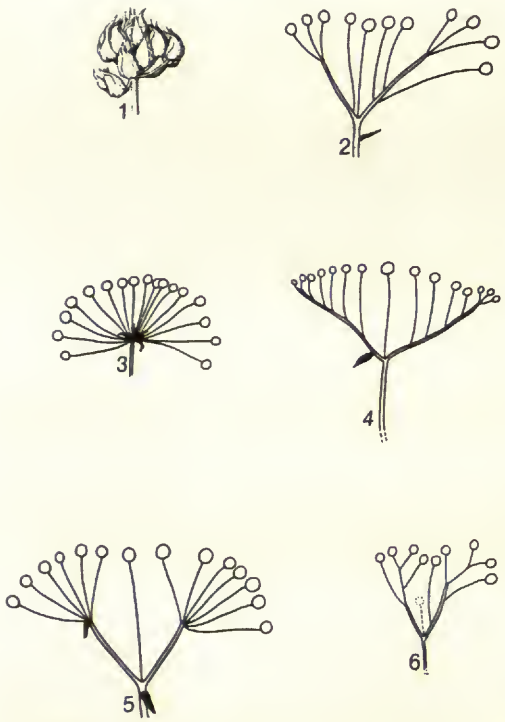

FIGURE 3. Types of inflorescence found in *Dombeya burgessiae*.—1. Ovoid-acute juvenile inflorescence (*Seyani & Patel* 955).—2. Corymbose cyme (*Galpin 804*).—3. Simple umbel (*Richards 9912*).—4. Corymbose cyme (*Galpin 804*).—5. Bi-umbellate inflorescence (*Chapman 169*).—6. Corymbose cyme (*Seyani & Patel 995*).

states. The table is large and complicated and is not presented here.

Indumentum characters had been used to discriminate between species in the past. Four such characters were scored for one specimen per degree square and the data was displayed symbolically on a map (Fig. 1). If two or more specimens were available from the same degree square, in order to avoid bias the specimen chosen was that whose collector's name came first in an alphabetical sequence.

The greenhouse growth experiments were carried out at the Botany School greenhouses, Oxford University. Characters such as germination type, cotyledon type, flower color, etc., were studied under similar environmental conditions.

OBSERVATIONS

The analysis of variation of the morphological characters has shown that the *Dombeya burgessiae* complex is a very variable group. The visual inspection of the results of the tabulation of 23 characters with 93 states alone was sufficient to show that variation in the characters was poorly correlated both among the characters themselves and with geography. Great variability was noticed in leaf shape (Fig. 2), flower color (ranging from white to pink, with or without a red center or veins), inflorescence branching (Fig. 3), and especially in the quality and density of the indumentum. The leaf outline and indumentum contribute greatly to the visual appearance of the plant, and these characters, particularly the latter, have been used in the past to distinguish several 'species' in the complex (Wild, 1961). Indeed, if a few specimens are chosen at random, at first it is often difficult to believe that they could belong to the same species. A thorough analysis of the variation in these and other characters throughout the geographical range of the species has, however, demonstrated that the pattern of variation is too poorly structured to justify the recognition of more than one taxon.

The scoring of four indumentum characters (Fig. 1) shows poor correlation. Variation in indumentum is chiefly in the length of the hairs and their density, not in the basic type of trichome. Such variation is probably controlled by few genes or highly affected by some ecological and/or environmental factors. Furthermore, some striking variants appear to have arisen polytopically, e.g., the short whitish, tomentellous indumentum of the lower leaf surface characterizes populations in southern Tanzania (*D. burttii*), northeastern Zambia (*D. greenwayi*), central Malawi (*D. nyasica*), and the Barberton District, Transvaal (*D. pulchra*), while the rust brown, densely tomentose indumentum on organs characterizes variants in Vila Cabral, Mozambique, and northern Malawi (*D. johnstonii*), and southern Malawi (*D. calantha* and *D. lasiostylis*). Plants with quite glabrous stems and petioles are common in northern Zambia, northern Malawi, and southern Tanzania (*D. tanganyikensis* and some collections of *D. nyasica*).

It was frequently found that several striking variants can occur in a single degree square. While conducting work in Malawi, the author found variation in indumentum and flower color among plants growing within short distance of each other (e.g., *Seyani & Patel 845* a & b). The above observations and the data presented in Figures 1–3 clearly show that variation is kaleidoscopic and that similar phenotypes can occur in widely separate localities.

In view of the great variation in *Dombeya bur-*

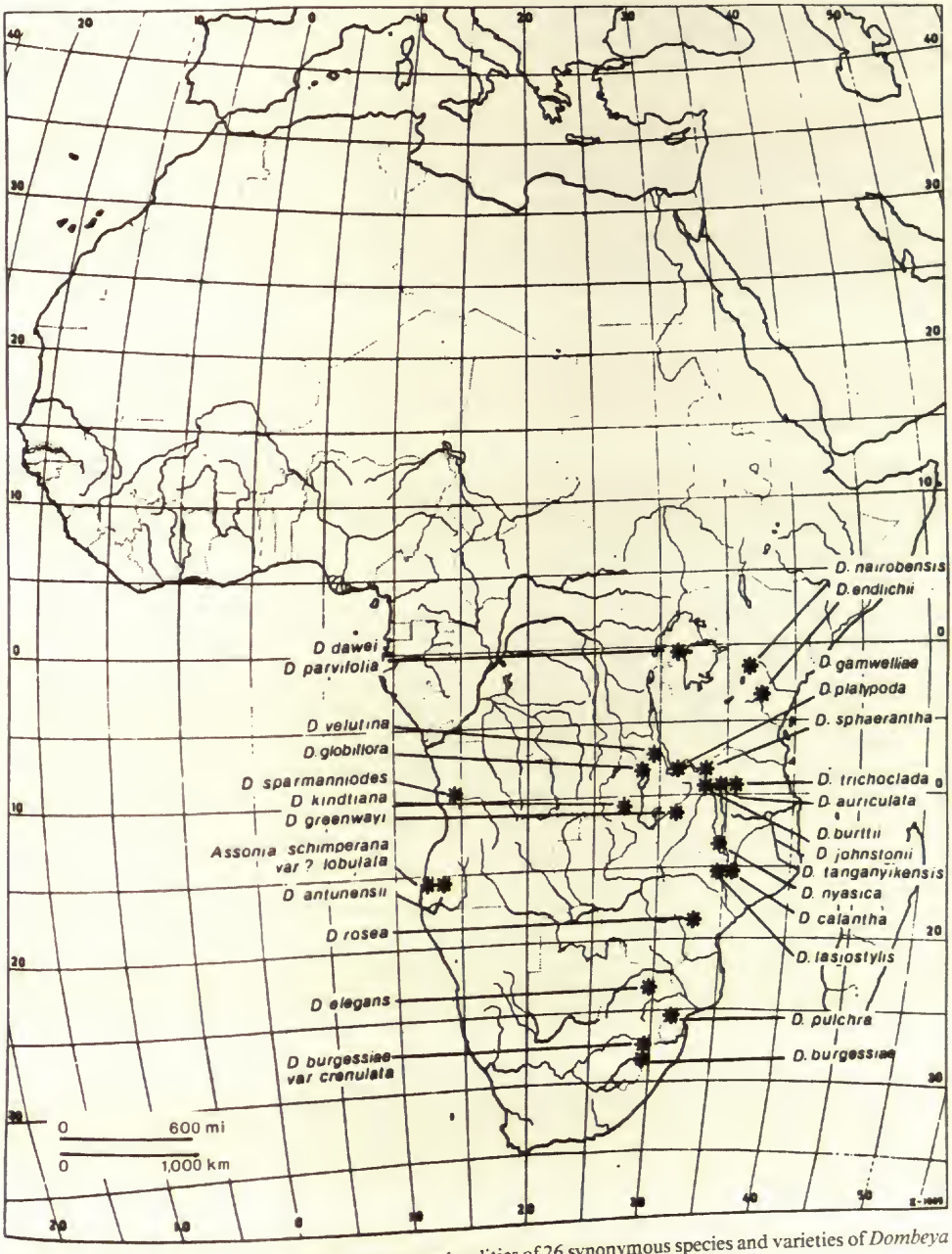

FIGURE 4. A distribution map showing the type localities of 26 synonymous species and varieties of *Dombeya burgessiae*.

gessiae, it is not surprising that, as interpreted here, it should have many synonyms. The type localities of 26 synonymous species and varieties (Fig. 4) show that in nearly every part of its range local populations have been accorded specific or, more rarely, varietal rank. The data from greenhouse plants did not differ much from those obtained from field or herbarium studies. However, in germination experiments it was found that some seeds have subhypogeal germination while others have epigeal germination. Similar inconsistent behavior is displayed by the West African

D. buettneri K. Schum, suggesting that this character has virtually no taxonomic significance in *Dombeya*.

Taxonomy and Species Description

The results of this study show that the pattern of variation in the *Dombeya burgessiae* complex is poorly structured. The many variants that have been given different names in different parts of Africa (Fig. 4) are part of a wider variation of *D. burgessiae* and as such cannot be kept as separate taxa. These names represent populations that are conspecific with *D. burgessiae* and are here put into synonymy. *Dombeya burgessiae* is now treated as follows.

Dombeya burgessiae Gerrard ex Harv., Fl. Cap. 2: 590. 1862. Harv., Thes. Cap. 2: 24, t. 137. 1863. Mast., Fl. Trop. Africa 1: 228. 1868. K. Schum., in Engl., Mongr. Afrik. Pflanzen-Fam. 5: 28. 1900. Wild, Fl. Zambesiaca 1: 522. 1961. Bamps, Fl. Congo Rwanda Burundi 10: 246. 1963. *Assonia burgessiae* (Gerrard ex Harv.) Kuntze, Revis. Gen. Pl. 1: 76. 1891. TYPES: South Africa, *McKen s.n.* (TCD, syntype); *Gerrard s.n.* (TCD, lectotype).

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Dombeya nyasica Exell, J. Bot. 77: 166. 1939. Wild, Fl. Zambesiaca 1: 523. 1961. TYPE: Malawi, *Burtt 6085* (BM, holotype; BR, K).

Dombeya burttii Excell, J. Bot. 77: 165. 1939. TYPE: Tanzania, *Burt 6154* (BM, holotype; K).

Dombeya greenwayi Wild, Bol. Soc. Brot., Sér. 2, 23:

35. 1959. Fl. Zambesiaca 1: 521. 1961. TYPE: Zambia, *Greenway 5527* (K, holotype).

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Shrub 2–4(–6) m tall. *Branchlets* tomentose, densely pubescent, or glabrescent. *Trichomes* of simple and stellate, acicular hairs, and minute, subsessile, short-stalked and long-stalked, glandular hairs. *Leaf lamina* 11–23 × 7–18(–23) cm, nearly always distinctly 3-lobed, rarely 5-lobed or unlobed, apex usually distinctly acuminate; margin rather coarsely and irregularly crenate or dentate; base 5–9-nerved, deeply cordate; upper surface sparsely to densely pubescent, tomentose or tomentellous; lower surface usually densely pubescent, tomentose or tomentellous, with mostly long-armed hairs; *petiole* (4–)7–15 cm long; *stipules* (0.4–)0.8–1.3(–2.5) × 0.3–0.6(–1.2) cm, ± lanceolate to broadly ovate, long-acuminate. *Inflorescence* 6–21(–28) cm long, axillary, corymbose umbellate, biumbellate, or subumbellate, usually many-flowered; peduncle 3.8–16.5 cm long, slender or stout, sparsely to densely pubescent; peduncle bracts 1.05–1.2 × 0.53–0.74 cm, inserted at or below the apex of the peduncle, ovate-acuminate, pubescent or glabrescent, very caducous; sub-branches absent or present, branched or condensed; sub-branch bracts caducous or absent; pedicels 2.2–3.8 cm long, slender or stout. Epicalyx bracts 1–1.4 × 0.2–0.5 cm, at calyx base, rarely on short calyx-stipe, variable in shape, acute to long-acuminate, caducous. *Sepals* 0.9–1.7(–2.1–2.3) × 0.2–0.8 cm, lanceolate, acute, pubescent outside, reflexed after anthesis. *Petals* (1–)1.2–2.5(–2.8) × 1–2.5(–3.3) cm, pink or white, with or without a red center or veins, spreading after anthesis. *Androecium* 1–2 cm long; staminal tube (1.2–)1.5–5 mm long, utriculiform or ± coroniform; staminodes 7–1.6(–2) × 1–2 mm, linear-oblanceolate to linear-spathulate; longest stamen 6–10(–2.5) mm; anthers 2–5 mm long, apex blunt rarely apiculate. *Ovary* ovoid-globose, tomentose, loculi glabrous or pubescent within; ovules (2–3–)4–8(–9) per loculus; style 5–16 mm long, filiform or stout, pubescent or glabrous; stigmatic arms with or without a few stellate trichomes. *Capsule* ovoid or globose, 0.5–1.5 cm in diameter, tomentose. Seeds 3–35 × 2–22 mm, dark brown to black.

Relationship with Other Taxa

In subgenus *Dombeya*, *D. burgessiae* is closely related to *D. buettneri*. However, *D. burgessiae* can be distinguished from the latter by its leaf apex, which is nearly always more finely drawn out, and the base, which is much more deeply cordate. The peduncle is always shorter than the petiole, which in *D. buettneri* is usually longer. The only glandular hairs that have been observed in the leaves and pedicels of *D. buettneri* in the area of overlap are subsessile, while in *D. burgessiae* long-stalked glandular hairs are also nearly always present, except in a few individuals where they are replaced by short-stalked glandular hairs.

There are also a few species that resemble *Dombeya burgessiae*, notably *D. acutangula* Cav., *D. torrida* (J. F. Gmel.) P. Bamps, and *D. wittei* De Wild. *Dombeya acutangula* differs from *D. burgessiae* in its closely striate second-year branchlets and in its subtruncate to shallowly cordate leaf base. The cincinnate inflorescence and the suborbicular median epicalyx bracts of *D. acutangula* are unique in the genus.

Dombeya torrida differs from *D. burgessiae* in habit, being a tree not a shrub; in leaf outline, usually unlobed (exceptionally with two vestigial lateral lobes), apex rather suddenly and finely accuminate, usually broadest near the base; leaf venation with tertiary nerves parallel and closely set; leaf indumentum scabridulous and with shorter hairs on both surfaces, long-stalked glandular hairs usually absent, dense long pilose hairs frequently occurring at apex of petiole and at base of lamina beneath; unexpanded inflorescence rounded, not acute.

Dombeya wittei differs from *D. burgessiae* in its smaller, strictly unlobed leaves with more regularly toothed margins. In addition, nearly all specimens examined of *D. burgessiae* have more flowers.

Distribution and Ecology
(Figs. 1, 4)

Dombeya burgessiae extends from Uganda and Kenya southward to Swaziland and Natal, and westward across the Zaire–Zambezi watershed into Angola. It is a characteristic member of the Afromontane flora, which also has scattered, distant satellite populations in lowland areas. On the mountains it ascends to more than 2,300 m, and its most frequent habitats are the forest edge and areas in early stages of forest regrowth. Away from the mountains it descends to about 800 m in tropical Africa. In these lowlands it appears to be rare and is mostly confined to the edges of

riparian forest or the rocky banks of rivers. Further south in Mozambique and Natal it descends almost to sea level.

Specimens examined. ZAIRE. SE 0629: Mt. Zawa, *Delvaux 559* (BR). SE 0727: Upemba, Kabongo–Kasiba, 1,250 m, *De Witte 6372* (BR). SE 0729: Marungu, Katomia, *Vandenbrande 101* (BR). SE 0827: Lusinga, 1,800 m, *De Witte 2339* (BR). SE 0828: Lukonzolwa, *Quarré 3294* (BR, holotype of *D. globiflora*). SE 0922: Mwene Djamba, *Risopoulos 818* (BR, K, WAG). SE 0926: Lukoka R., Ganza, *De Witte 6763* (BR, K). SE ?0927: Kundelungu, 60 km from the southern edge, *Schmitz 4920* (BR). SE 1022: Dilolo, *Young 164* (BM, BR). SE 1027: Lukafu, Kankima Gorge, *Quarré 5524* (BR, WAG).

RWANDA. SE 0130: L. Ihema, Nyakakondje, 1,250 m, *Robyns 4048* (BR).

UGANDA. NE 0030: Kisomoro, 2,130 m, *Hazel 208* (K). NE 0134: Mt. Kadam (Debasien), 2,440 m, *Eggeling 2835* (K). NE 0234: Napak Mt., 1,980 m, *Thomas 3609* (K). NE 0331: Otzi F.R., 1,220 m, *Dawkins 298* (FHO, K). SE 0029: Nyakagyeme, *St. Clair-Thompson 1765* (FHO). SE 0030: Mbarara-Toro, *Gibson 409* (BR, K). SE 0031: Buddu, *Scott Elliot 7475 bis* (K, holotype of *D. parvifolia*).

KENYA. NE 0034: Kakamega, *Perdue & Kibuwa 9490* (BR, K, LISC). NE 0035: near Eldama Ravine, 1,820 m, *Drummond & Hemsley 4432* (BR, K). NE 0037: Mt. Kenya, Ndare Forest, 1,675 m, *Porter 767* (FHO). NE 0134: NE Mt. Elgon, 2,285 m, *Dale 808* (FHO). SE 0035: Maji Mazuri, 2,400 m, *T. A. Angus 699T* (BR, FHO). SE 0036: Naivasha, *Wimbush 928* (FHO). SE 0037: Mt. Kenya, Irangi, 1,980 m, *White 1071* (BM, BR, FHO). SE 0134: Lolgorien, 1,830 m, *Glover et al. 654* (BR, K). SE 0135: Ngore Ngore, *Rammell 1002* (FHO). SE 0136: Nairobi, Muthaiga, 1,700 m, *Piemeisel & Kephart s.n.* (BR).

TANZANIA. SE 0134: Chamliho, 1,390 m, *Tanner 1696* (BR, K, WAG). SE 0232: Katungulu, 1,150 m, *Tanner 1581* (BR, K). SE 0234: Ikoma, Manjira, 1,370 m, *Tanner 4453* (BR, K, WAG). SE 0335: Ngorongoro Crater, *Pole-Evans & Erens 894* (BR). SE 0336: Engare Olmotoni 1,620 m, *Baldwin 1* (BR, K). SE 0337: Kilimanjaro, Marungu, 1,200 m, *Volkens 2242* (BR). SE 0629: Pasagulu Mt., Musenabantu, 1,620 m, *Harley 9289* (BR, K). SE 0731: Mbisi Forest, 2,100 m, *Richards 13089* (BR). SE 0833: Poroto Sawmill, 1,800–2,000 m, *St. Clair-Thompson 759* (K). SE 0835: Mufindi, *Pitt-Schenkel 468* (FHO). SE 0933: Mporoto Mts., 2,130 m, *Burtt 6154* (BM, holotype of *D. burttii*; K). SE 0934: Lisitu-Lugalawa, 1,800 m, *Thulin & Mhoro 1138* (K). SE 1034: Upangwa, *Wigg 54* (FHO). SE 1134: Lupembe Hill, 1,800 m, *Milne-Redhead & Taylor 10255* (BR, K, LISC).

MOZAMBIQUE. SE 1234: Maniamba, *Pedro & Pedrogão 3779* (LMA, MAL). SE 1235: Lualezi R., Vila Cabral, Lake Malawi, 1,180 m, *Mendoça 725* (K, LISC). SE 1335: Vila Cabra, Lichinga, *Torre 4* (COI, LISC). SE 1432: Marávia, Vila Vasco da Gama, *Andrada 1677* (LISC). SE 1434: Angónia, Vila Mousinho, *Mendoça 4211* (BM, BR, LISC). SE 1437: Malema, Mutuali, *Mendonça 2299* (BR, LISC). SE 1438: Mt. Ribáuè, 900 m, *Gomes & Sousa 867* (K). SE 1531: Fingoè, 900 m, *Torre 3238* (BR, K, LISC, SRGH). SE 1532: Chicoa-Fingoè, 70 km, *Barbosa & Carvalho 3311* (LMU, MAL). SE ?1536: Nhamarroi-Ile, *Torre 5475* (K, LISC). SE 1538/1639: Murrupula, R. Ligonha, *Torre 615* (LISC). SE 1636: Namagoa, 60–120 m, *Faulkner 92* (BM, BR, K). SE 1637: Muzo Valley, 820 m, *Vasse 25* (P). SE 1733: Mt. Choa, 1,400 m, *Torre & Correia 18683* (BR, K, LISC). SE 1736: Cundine, *Le Testu 384* (BM, BR). SE 1832: Vumba Mts., 900 m, *Gomes & Sousa 4779* (K). SE 1833: Chimoio, perto do R. Vanduzi, *Andrada 1202* (LISC). SE 1834: Gorongosa, Morumbozi, *Macedo & Balsinhas 1642* (LMU, MAL). SE 1933: Mavita, R. Rutanda, *Barbosa 1707* (LISC). SE 2032: Spungabera (Espungabera), 1,000 m, *Torre 4291* (LISC, WAG). SE ?2033: Gogoi, Lucite R., *Pedro & Pedrogão 7535* (LMU, MAL). SE 2532: Namaacha, R. Impamputo, *Barbosa & Lemos 7514* (K, LISC). SE 2632: Lebombo Mts., Estatuene, *Gomes & Sousa 3734* (K).

MALAWI. SE 0933: Mafinga Mts., W of Chisenga, 1,670 m, *Tyrer 518* (BM, BR). SE 1033: Nyika Plateau, 2,300 m, *Robinson 6242* (K). SE 1133: Vipya Plateau, 51 km SW of Mzuzu, 1,730 m, *Pawek 8753* (K). SE 1334: Ntchisi Mt., 1,650 m, *Burtt Davy 21125* (FHO). SE 1433: Dzalanyama F.R., 1,280 m, *Brummitt et al. 14942* (K). SE 1434: Dedza Mt., 1,860 m, *Burtt Davy 21569* (FHO). SE 1534: Dzonze Mt., *Chapman 1351* (FHO, K). SE 1535: Zomba, *Whyte & McClounie s.n.* (K, holotype of *D. calantha*). SE 1634: Manganja Hills, *Meller* (K). SE 1635: Cholomwani, *Topham 698* (FHO).

ZAMBIA. SE 0831: 13 km NW of Mbala, 1,340 m, *Hutchinson & Gillett 4011* (BM, K). SE 0933: Mafinga Mts., *Lawton 471* (K). SE 1032: Isoka, *Fanshawe 12003* (K). SE 1033: Nyika Plateau, near Chowo Rock, 2,130 m, *White 2568* (BR, FHO, K). SE 1124: Mwinilunga District, Matonchi R., *Milne-Redhead 4582* (BM, BR, K). SE 1131: Shiwa Ngandu–Mpika, 48 km, *Angus 874a* (FHO). SE 1423: Kabompo mouth, 970 m, *Gilges 370* (K).

ZIMBABWE. SE 1831: Marandellas, 1,600 m, *Eyles 4378* (K). SE 1832: Inyanga, Mt. Mimunzi, 1,900 m, *Bamps et al. 256* (BR). SE 1932: Umtali–Vumba, km 16, *Loveridge 1086* (BR). SE 2030: Zimbabwe Ruins, *Hutchinson & Gillett 3320* (BM, K).

ANGOLA. SE 0614: Lufinde Valley, 500 m, *Dawe 124* (K). SE 0914: Golungo Alto, Cacarambola, *Welwitsch 4734* (BM, holotype of *D. sparmannioides*; BR, K). SE 0915: Pungo Andongo, *Mechow 147* (BR). SE 1114: Seles, Bimba, 1,000 m, *Gossweiler 9371* (BM, K). SE 1215: Cuito R., Quipeio, 1,500 m, *Exell & Mendoça 1878* (BM, LISC). SE 1413: Vila Arriaga, Bibala, 900 m, *Gossweiler 13365* (LISC). SE 1513: Serra de Chela, Bruco, Tyivinguiro, *Mendes 921* (LISC, WAG).

SWAZILAND. SE 2531: Piggs Peak, 915 m, *Compton 27620* (K). SE 2631: Hlatikulu, Kubuta Estate, *Pierce 9* (BR).

SOUTH AFRICA. SE 2229: Wyliespoort, *Van Graan & Hardy 504* (K, WAG). SE 2230: Messina, *Pole-Evans 1447* (K). SE 2231: Punda Maria, *van der Schijff 2924* (K). SE 2329: Louis Trichardt–Mara, km 10, *Meeuse 10209* (FHO, K). SE 2430: Bourkes Luck Mine, 1,700 m, *Galpin 14269* (K). SE 2530: Lydenberg, *Wilms 78* (BM, BR, K). SE 2531: Barberton, *Holland s.n.* (BM). SE 2729: New Castle, *Rehmann 7049* (BM, K, isotype of *D. burgessiae* var. *crenulata*). SE 2831: Hlabisa, 390 m, *Codd 9612* (K).

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PHYTOGEOGRAPHY OF *RAPHIONACME* HARV. (PERIPLOCACEAE)[1]

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ABSTRACT

Raphionacme is an African genus of 31 species, the majority of which are geophytic herbs. A few are geophytic climbers. It is widely distributed in Africa, occurring in the Zambezian and Sudanian domains of the Sudano–Zambezian Region in particular, and with the main concentration of species in the subtropical southeastern and eastern areas. Four sections are recognized in *Raphionacme*. The distribution of each section and the geographical concentration of species within each section are discussed in detail and are related to environmental and climatic factors that may determine distribution patterns.

RÉSUMÉ

Le *Raphionacme* est endémique à l'Afrique. Le genre comporte 31 espèces dont la majorité sont des espèces suffrutescentes. Quleques unes sont des plantes suffrutescentes grimpantes. Les auteurs montrent que *Raphionacme* est largement réparti dans tout l'Afrique; on le trouve dans les domaines de Zambézie et du Soudan en particulier, avec une concentration principale d'especes dans la région sud-est. On peut distinguer quatre sections dans *Raphionacme*. Les auteurs discutent à l'aide de cartes de la répartition de chaque section et de la concentration géographique dans les sections. Ils mentionnent également les facteurs d'environnement et de climat qui peuvent déterminer la répartition de chaque section.

The Periplocaceae (Asclepiadaceae–Periplocoideae) are confined to the temperate and tropical regions of the Old World (Hutchinson, 1973) and includes approximately 40 genera and 200 species (Cronquist, 1981). It is well represented in Africa with approximately 20 genera and 70 species. The African Periplocaceae comprise woody forest climbers (some enormous lianas), woody shrubs (some of these facultative climbers) and *Raphionacme,* the sole herbaceous genus. Ornamental members of the family include species such as the beautiful *Cryptostegia grandiflora* (Roxb.) R. Br. ex Lindl. of the Mascarene Islands and Australia. The family is recognized by the flowers, which bear a variety of coronal forms and peculiar spathulate or oval pollen carriers.

Raphionacme is the largest genus of the African Periplocaceae and includes 31 species, all endemic to Africa. The genus was last comprehensively revised by Brown in 1902 and 1907 for the *Flora of Tropical Africa* and *Flora Capensis,* respectively. Bullock revised the genus partly for the *Flora of West Tropical Africa* in 1954 and 1963. The present authors are revising the genus for the *Flora of Southern Africa* and *Flora Zambeziaca.*

Schumann (1895) divided the genus into four sections. Even though only a small number of species were known at that time, his division was well founded and is followed in this presentation. The sections of *Raphionacme* are distinguished on the morphological structure of the inflorescence and flower and on the habit of growth.

Raphionacme consists of geophytic herbs and a few geophytic climbers. A large turnip-shaped underground root tuber is very characteristic of the genus (Fig. 1), hence the name *Raphionacme,* derived from the Greek name for the turnip. In most species of *Raphionacme* this tuber is edible and is utilized as food, medicine, or as a source of water. *Raphionacme hirsuta* (E. Mey.) R. A. Dyer seems to be the exception, since it is alleged that the tuber is poisonous. Like other Periplocaceae, *Raphionacme* produces a copious milky latex. At the beginning of the present century attempts were made to produce rubber from the latex extracted from the tuber of *R. utilis* N. E. Br. & Stapf, but this venture proved uneconomical. The flowers (Fig. 2) may be inconspicuously

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FIGURE 1. *Raphionacme hirsuta.* Large tuberous root crowned by stems and leaves.

small or they may be large and showy with colors that range from green and yellow to pink and purple. They are sweet scented and complex in structure, especially with regard to the gynostegium and corona. Although no evidence has yet been found, the way that the gynostegium and corona fit together suggests that insects with long probosci are the pollinators of *Raphionacme*. The fruits are solitary or paired hornlike follicles. The seeds possess comas of hair for wind dispersal.

The aim of this article is a presentation of the natural distribution of the genus and its sections through Africa, relating, where possible, these distribution patterns with prevailing environmental and climatic factors, species concentrations, and possible history of the genus.

FIGURE 2. *Raphionacme dyeri* in flower.

DISTRIBUTION

Widely distributed in Africa (Fig. 3), *Raphionacme* are always minor members of the plant communities in which they occur. The highest concentration of species and the most continuous distribution occur in the Zambezian and Usambaro–Zululand domains of the Sudano–Zambezian Region. Angola, Botswana, Malawi, Mozambique, South Africa (partly), South West Africa/Namibia (partly), Tanzania, Zaire (partly), Zambia, and Zimbabwe fall in these two domains. The highest concentration of species occur in Malawi, the eastern part of South Africa, and in coastal Tanzania (Fig. 3).

The Sudanian Domain (Sudano–Zambezian Region) represents the second main area of distribution (Fig. 3). The pattern of distribution is more discontinuous and the concentration of species is likewise lower than in the Zambezian Domain. Countries included are the Cameroons, Central African Republic, Chad, Dahomey, Ethiopia, Ghana, Guinea, Guinea Bissau, Ivory Coast, Mali, Niger, Nigeria, Senegal, Sierra Leone, Sudan, and Bourkina Faso.

In the Afroriental Domain, also part of the Sudano–Zambezian Region, species are fairly common in Kenya and Tanzania, but become rare northeastwards into Somalia. A single, totally isolated record exists for *Raphionacme madiensis* S. Moore from the far northeastern sector of Somalia. Only three scattered records exist for the Sahelian Domain of the Sudano–Zambezian Region. *Raphionacme brownii* Scott Elliott and *R. vignei* E. A. Bruce were collected in Chad, and *R. excisa* Schltr. was found in the Sudan. They represent the northernmost records for the genus (Fig. 3).

Raphionacme is scarce in the Congo Domain but more common in the Guinea Domain of the Guineo–Congo Region. The four species found in Ghana, together with the four species of Uganda, actually represent the highest concentrations of *Raphionacme* species north of the equator. Except for *R. michelii* Wildem., which was collected in the interior of Zaire, the few other species that occur in the Congo Domain are from the transition areas in the Cameroon, Zaire, Burundi, and Uganda.

In the Namib Karoo Region along the southwestern coast of Africa, there are a small number

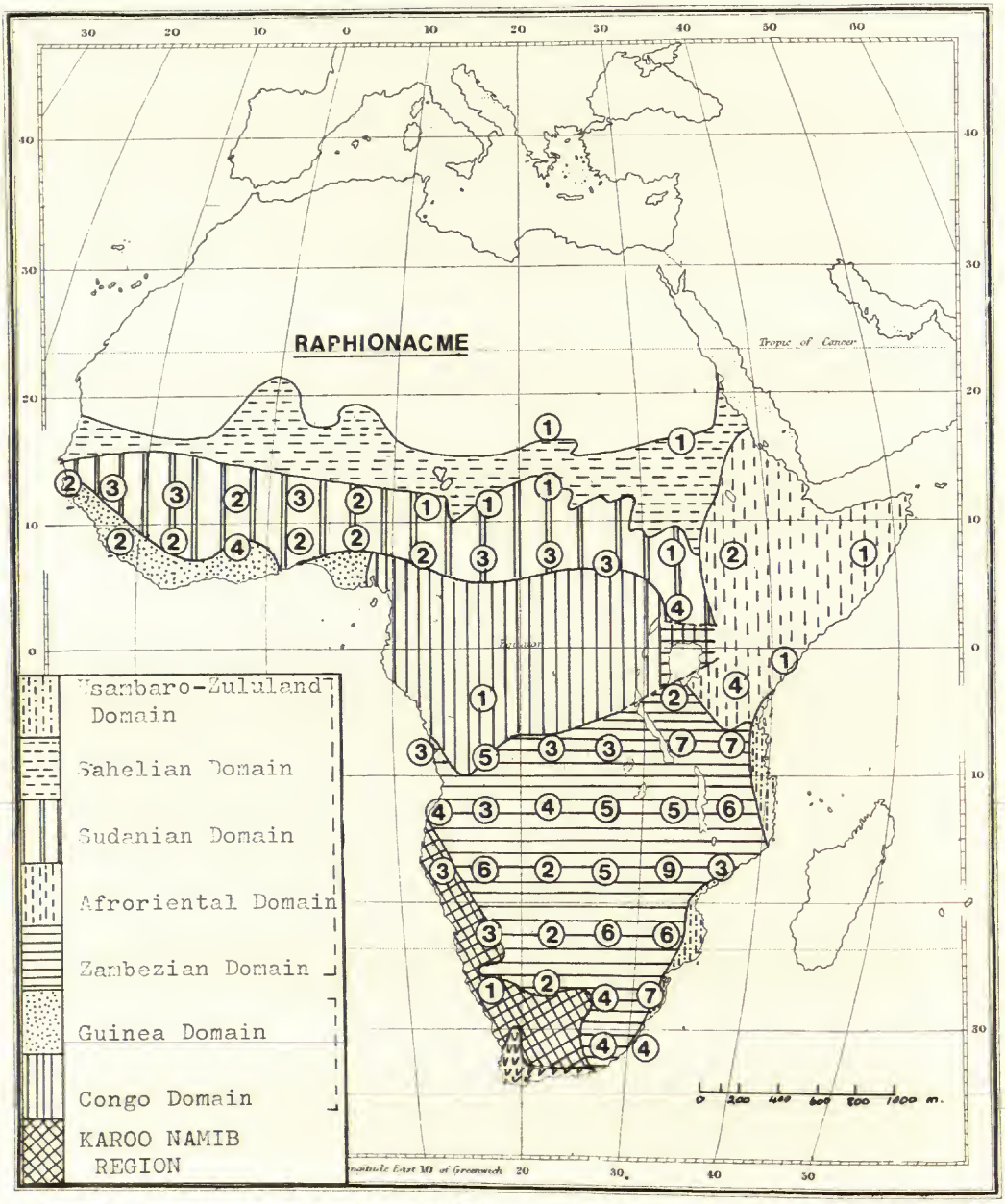

FIGURE 3. Phytogeographical distribution of *Raphionacme*. (Numbers represent species concentrations per 5° square; map after Brenan, 1978.)

of species of *Raphionacme*. Of these only *R. namibensis* Venter & Verhoeven occur in more or less true desert.

BIOCLIMATIC DISTRIBUTION AND ECOLOGY

In order to draw a correlation between the distribution of *Raphionacme* and the environmental and climatic factors that determine its distribution, the bioclimatic map of Phillips (1983) was used. His bioclimatic regions coincide to a large degree with the phytosociological regions of White (1971), refined by Brenan (1978), and as presented in Figure 3. The map of Phillips (1983), however, provides finer subdivisions and climatic correlations (Figs. 4–7). Table 1 sum-

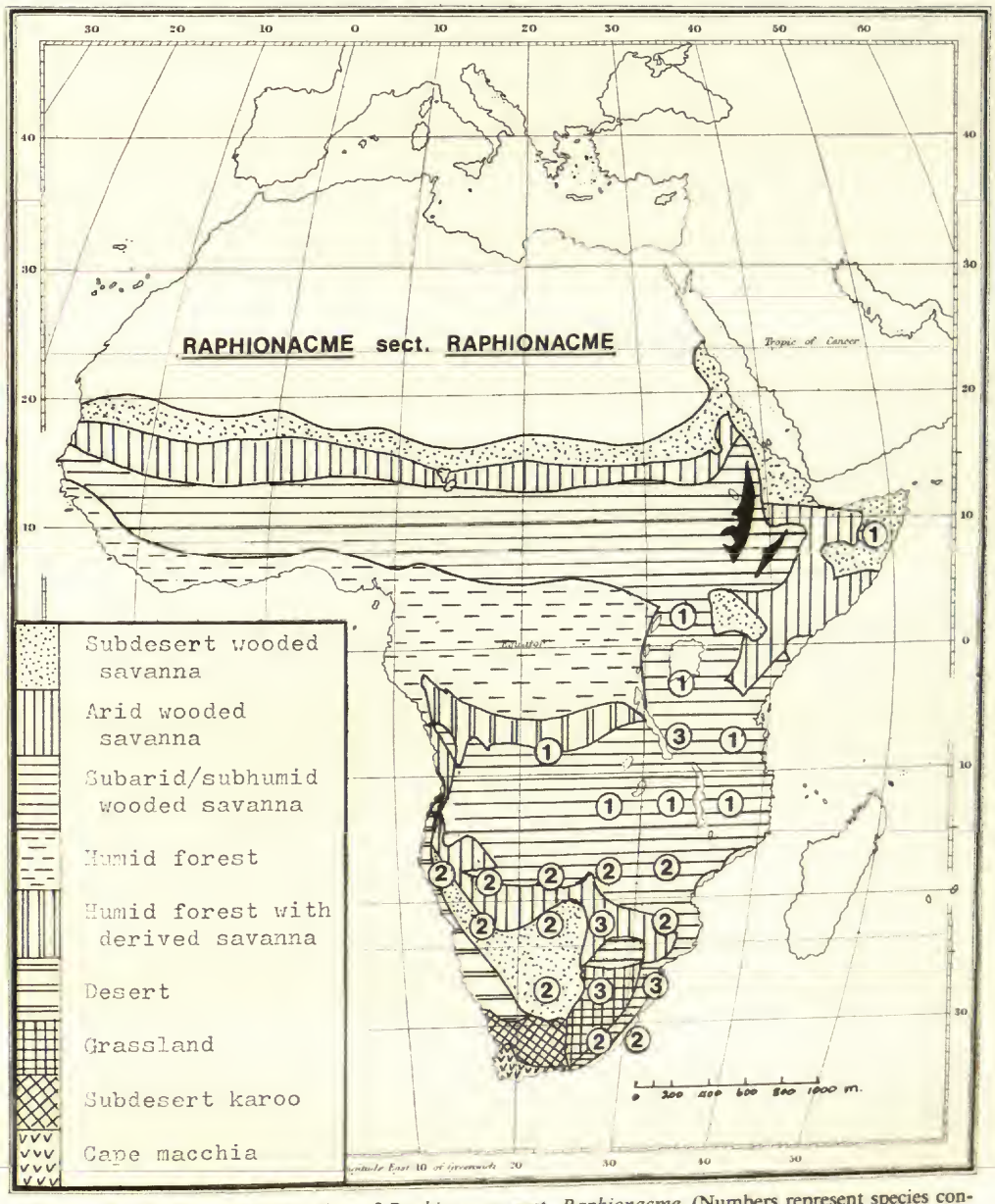

FIGURE 4. Bioclimatic distribution of *Raphionacme* sect. *Raphionacme*. (Numbers represent species concentrations per 5° square; map after Phillips, 1983.)

marizes the climatic factors as adapted from Phillips (1983) for the purpose of this paper.

Raphionacme sect. *Raphionacme* includes eight species. These are *R. dyeri* Retief & Venter, *R. hirsuta*, *R. lanceolata* Schinz, *R. longituba* E. A. Bruce, *R. madiensis*, *R. palustris* Venter & Verhoeven, *R. velutina* Schltr., and *R. zeyheri* Harv. All are erect or decumbent herbs. The section is restricted to southern and eastern Africa (Fig. 4). The main concentration of species are in the south, where they inhabit grassland, subdesert savanna, and arid to subhumid savanna. The climate ranges from arid (Table 1) in the west (*R. lanceolata*, *R. velutina*, and *R. zeyheri*) to relatively mild in the east (*R. palustris* and *R. hirsuta*). Frost may be a factor in higher altitude

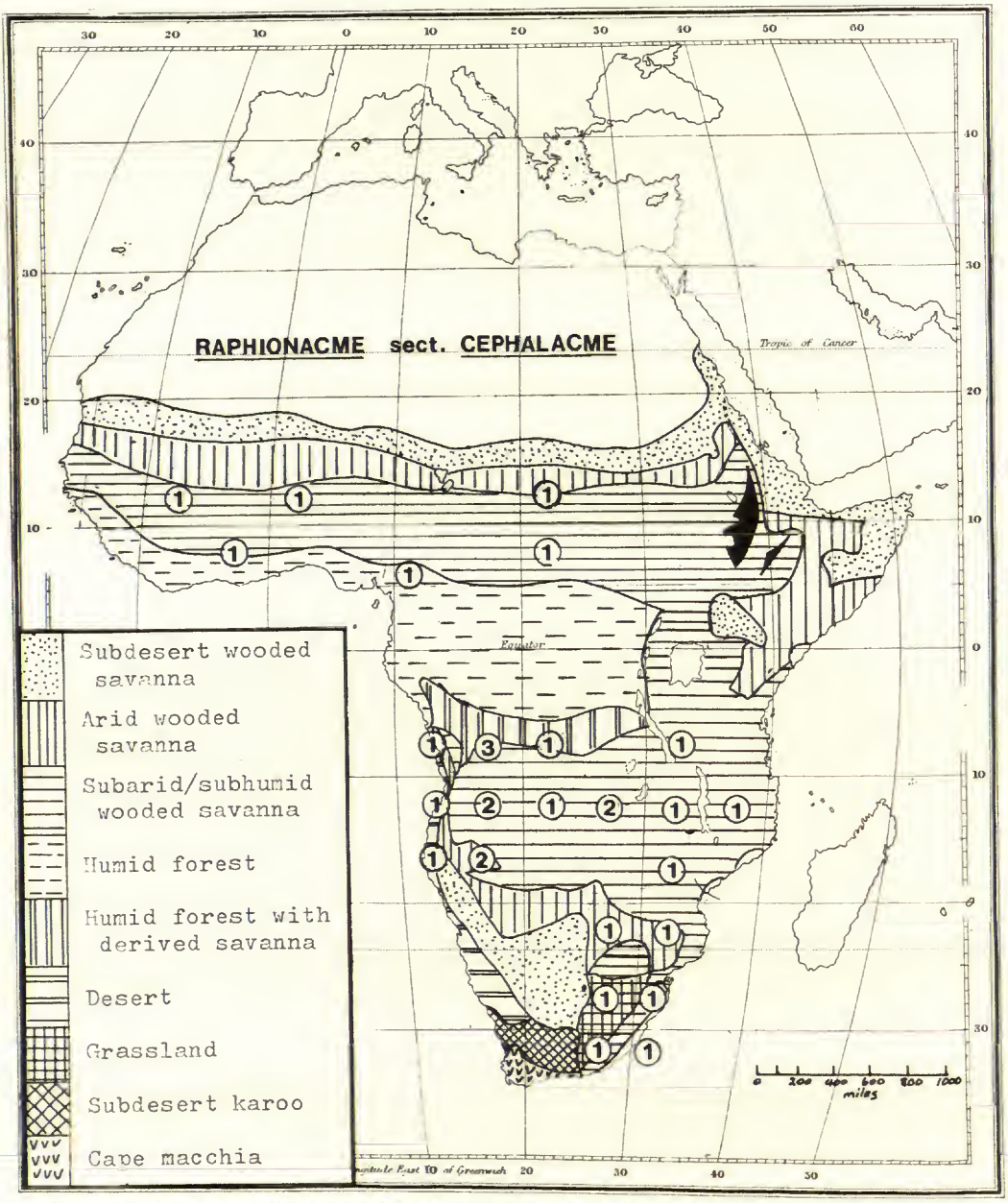

FIGURE 5. Bioclimatic distribution of *Raphionacme* sect. *Cephalacme*. (Numbers represent species concentrations per 5° square; map after Phillips, 1983.)

areas where *R. dyeri* and *R. hirsuta* occur. *Raphionacme palustris* grows in swamps or wet grassland. Northwards the section occurs in subarid to subhumid regions (*R. lanceolata, R. longituba* and *R. madiensis*), with the latter isolated in northeast Somalia. Although the overall climate suggests that the three last-mentioned species grow under milder conditions, collecting information indicates drier habitats such as shallow ground on rock. The section is found at altitudes that range from sea level (*R. palustris* and *R. hirsuta*) to as high as 2,300 m (*R. hirsuta*). *Raphionacme hirsuta, R. lanceolata* and *R. velutina* are the most widely distributed in section

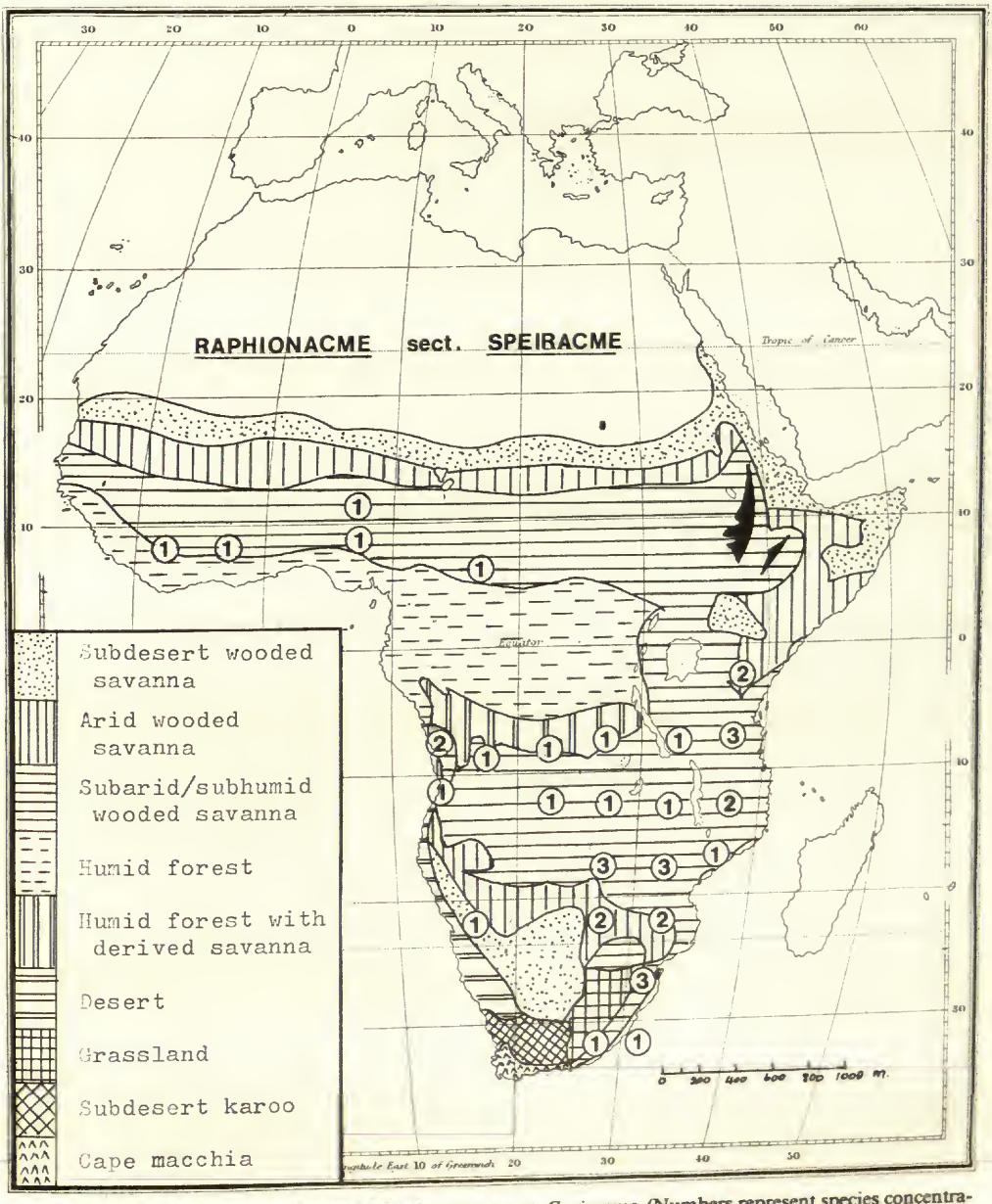

FIGURE 6. Bioclimatic distribution of *Raphionacme* sect. *Speiracme*. (Numbers represent species concentrations per 5° square; map after Phillips, 1983.)

Raphionacme, but none of the species occur over the full range of the section.

The species of section *Raphionacme* are all heliophytes growing on a variety of soils in either grassland or in the grass component of savanna. They flower from October to February, with a peak in December. *Raphionacme madiensis*, which spans the equator, has two flowering periods—in the south similar to the other members of the section and in the north from March to May.

Raphionacme section *Cephalacme* K. Schum. includes five species: *R. angolensis* (Decne.) N. E. Br., *R. galpinii* Schltr., *R. globosa* K. Schum.,

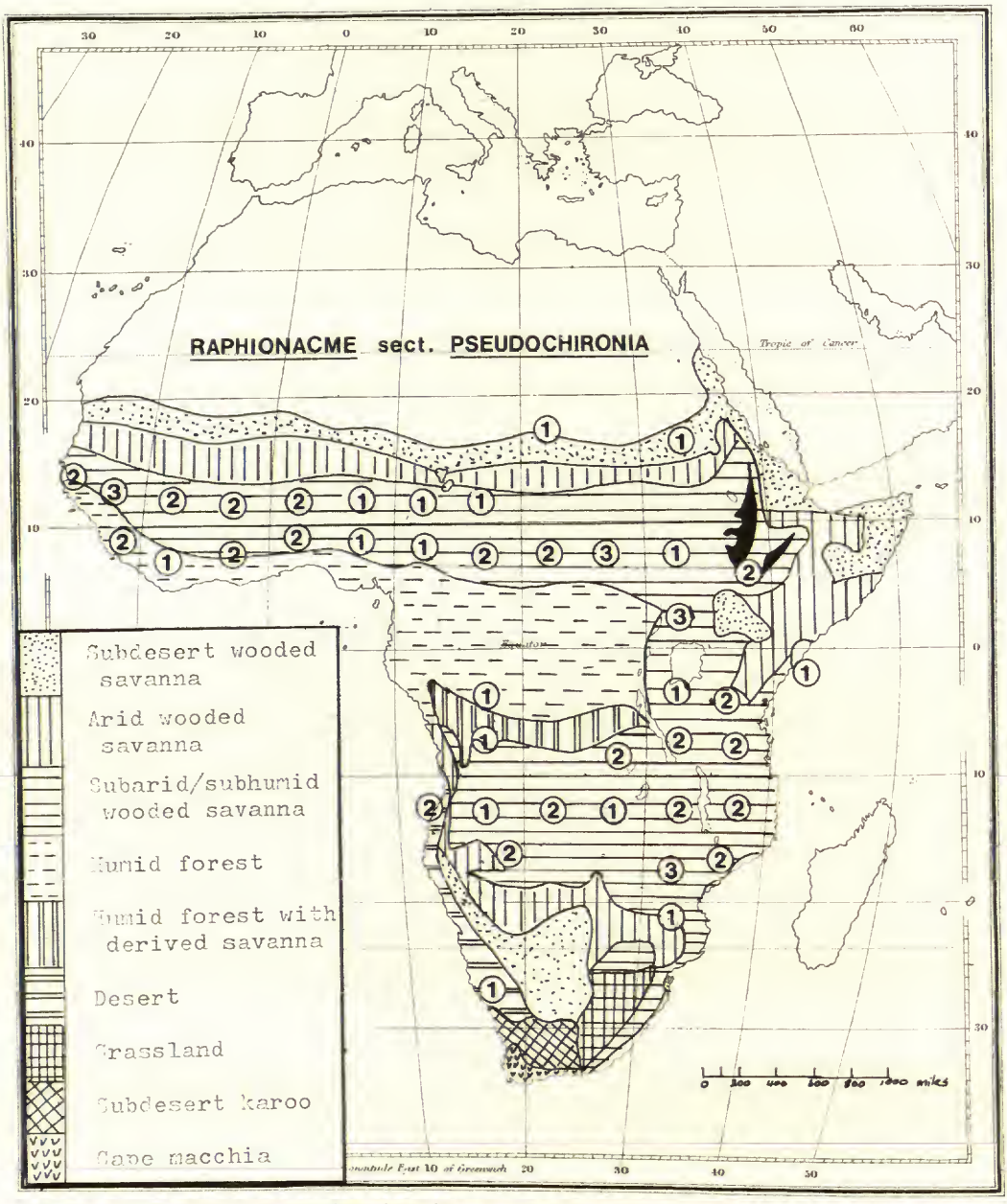

FIGURE 7. Bioclimatic distribution of *Raphionacme* sect. *Pseudochironia*. (Numbers on the map represent species concentrations per 5° square; map after Phillips, 1983.)

R. utilis, and *R. vignei*. These species are all erect herbs with their flowers borne in terminal, rather compact inflorescences. The section generally inhabits the milder subhumid parts of southern Africa, although *R. angolensis* and *R. globosa* also occur in the arid savanna of Angola (Fig. 5). *Raphionacme vignei* represents an isolated outlier north of the equator in the arid to subhumid savanna, but collection data indicate that this species grows on rocky outcrops in savanna, thus in drier conditions within the humid savanna. Similar information exists for the other species, and once again the conclusion may be drawn that the section in general is adapted to drier habitats.

TABLE 1. Climatic factors conditioning the bioclimatic regions inhabited by *Raphionacme* (from Phillips, 1983).

	Temperature °C (mean shade)	a) Humidity and b) Saturation Deficit, mb	Rainfall: Mean Annual, mm	Drought: Ecologically Dry Months (edm), Each with <25 mm Rainfall
Desert (Namib)	Mean maximum 27–29; absolute maximum 38+; frost in colder season	a) 13–20, rarely 20–27 b) 13–20	100–200(–350)	edm: 9–10
Subdesert wooded savanna	Megatherm 24–28, monthly maximum 30–34	a) 13–20, rarely 20–27 b) 13–20	50–200(–400)	edm: 9–11
Arid wooded savanna	Megatherm +23	a) 20–27 during rains; 13–20 during dry periods; b) 9–13(–20)	300–500, irregular, in poor season down to 100 mm	Frequent dry/hot spells, very severe; edm: 7–9
Subarid/ subhumid wooded savanna	Megatherm +23	a) 20–27 during rains; 13–20 during shorter dry periods; b) 7–9 (subhumid) to 9–13(–16) (subarid)	900–1,400(–1,800) (subhumid) to 400–600 (subarid); regular to irregular	Moderate to fairly long and severe; edm: 4–7
Humid forest (highly humid included)	Megatherm +23; annual and daily range slight	a) 20–27+; b) 1–4(–7)	1,800–2,500+, regular to moderately regular	Nil to rare, short and mild
Grassland	Mean minimum 4–8, frost severe to moderate; monthly mean maximum Dec./ Feb. 18–23	a) 13–20(–27); b) 4–9(–13)	(250–)500–750(–1,000)	edm: 5–8 and severe, to 1–3 and not severe

Altitudinally the members of section *Cephalacme* occur from sea level (*R. galpinii*) to approximately 2,000 m (*R. galpinii* and *R. globosa*). All species of the section are heliophytes and grow in grassland or the grassland component of savanna. Except for *R. vignei*, which flowers in April and May, they flower from September to February, with the peak in December.

Raphionacme section *Speiracme* K. Schum. comprises seven species. Four are climbers, namely *R. flanaganii* Schltr., *R. longifolia* N. E. Br., *R. monteiroae* (Oliv.) N. E. Br., and *R. welwitschii* Schltr. & Rendle. *Raphionacme procumbens* Schltr. is a prostrate plant under natural conditions, but it becomes a climber when grown in the glasshouse. *Raphionacme keayi* Bullock is the only nonclimber in the section, but only a few specimens exist and more collections may well indicate the existence of the climbing habit. In *R. longifolia* and *R. welwitschii* both the erect and climbing forms occur.

The environmental conditions under which this section is found are similar to those of section *Cephalacme* (Fig. 6). With the exception of *Raphionacme keayi*, species occur in scrubbier veld than those of section *Cephalacme*. The species scramble over tall grass, smaller trees, and shrubs in a variety of savanna communities. *Raphionacme monteiroae* is only found in arid to subdesert savanna and is widely but discontinuously distributed from Maputo (Mozambique) and Dar es Salaam (Tanzania) in the east to Okahandja (Namibia) and Loanda (Angola) in the west. The altitudes at which the species are found range from sea level (*R. monteiroae* and *R. flanaganii*) to approximately 1,800 m (*R. welwitschii* and *R. procumbens*). *Raphionacme procumbens* is concentrated to mountainous regions of higher altitude. Species flower from September to February, with November/December the peak flowering period. *Raphionacme monteiroae*, however, seems to be without a specific seasonal flowering period. Infrequent periods of rain in the arid places where it grows possibly act as a trigger mechanism for flowering, rather than the seasons. *Raphionacme keayi*, which occurs north of the equator (Fig. 6), flowers in June and July.

Raphionacme section *Pseudochironia* K. Schum. is the largest section, with 11 species, and it has the widest distribution of the four sections. It is also the most tropical section (Fig. 7) and comprises *R. brownii, R. caerulea* E. A. Bruce, *R. chimanimaniana* Venter & Verhoeven, *R. bingeri* (A. Chev.) Lebrun & Stork, *R. excisa, R. grandiflora* N. E. Br., *R. linearis* N. E. Br., *R. michelii, R. namibensis* Venter & Verhoeven, *R. splendens* Schltr., and *Raphionacme*, sp. nov. The flowers in the section are the most conspicuous in *Raphionacme*, with *R. splendens* and *R. linearis* undoubtedly the most beautiful species.

Section *Pseudochironia* in general inhabits savanna with the highest concentration of its species in Guinea, the Central African Republic, Uganda, and Malawi. They occur in a variety of habitats, ranging from clayey pans and sandy flats to rocky outcrops or mountainous veld. It is, however, remarkable that some of these species, especially *R. bingeri* and *R. excisa*, occur in "seasonally inundated savanna," "stony boggy soil overlying rock" or "rock pans with shallow soil." *Raphionacme linearis* is a marsh herb while *R. namibensis* is a xerophyte of desert habitats.

The section occurs from sea level (*Raphionacme excisa* and *R. splendens*) to approximately 1,500 m (*R. chimanimaniana, R. linearis*, and *R. splendens*). Of the southern species, *R. chimanimaniana* and *R. linearis* flower from October to February, but *R. splendens* flowers from July to September. The northern hemisphere species *R. brownii, R. bingeri*, and *R. michelii* flower from March to June. *Raphionacme excisa* spans the equator and flowers from February to April in the north and from September to December in the south. In contrast to the other sections of *Raphionacme*, some of the species of section *Pseudochironia* are precocious, forming leaves only after having flowered.

Discussion

Raphionacme is widespread over Africa in savanna or grassland (Figs. 3–7) in areas that have a climate ranging from very arid to fairly humid, but in general the genus tends to grow in drier habitats. Two species are exceptional and grow in swamps. All the species are geophytes with large root tubers. The genus is furthermore heliophytic and often pyrophytic. The majority are herbs, while a small number are climbers. The members of the genus are always lesser components of the communities in which they occur.

Section *Pseudochironia* includes the largest number of species and also has the widest distribution of the four sections of *Raphionacme*. Section *Raphionacme* is the second largest section and is concentrated in the southeastern part of the continent. Sections *Cephalacme* and *Speiracme* have their main centers of distribution in the subtropical part of southern Africa.

Altitude does not seem to be a critical factor

in the occurrence of the species of *Raphionacme*. *Raphionacme procumbens*, however, is fairly restricted to higher mountain habitats.

Comparing the intricate flowers and the herbaceous and geophytic habit of growth of *Raphionacme* with the simpler flowers and climbing or shrubby growth form of the other African genera of the Periplocaceae, one may make the conclusion that *Raphionacme* is the most specialized genus in the family. *Raphionacme* may have developed from such ancient climbing stock, with the climbing habit still present in section *Speiracme*. The change to the herbaceous and geophytic habit may have been initiated during the Tertiary in the late Eocene (38 million years ago), when drier climate began to spread over the middle latitudes of Africa (Axelrod & Raven, 1978). Other genera of the Periplocaceae possessing the climbing habit are still present in rain forests or riverine forest of drier areas. The establishment of open seasonally dry habitats during the Oligocene favored adaptations towards geophytism and deciduousness (Goldblatt, 1983), and it may be a likely period in which *Raphionacme* evolved and radiated over Africa. It is impossible to identify the area of origin. If species density is any indication of such an area of origin, then southeast Africa seems to be the likeliest place, but such an assumption is dangerous. Major climatic changes are certain to have had important impact on the distribution of plants (White, 1971).

The present discontinuous distribution of species in sections *Cephalacme* and *Speiracme* (Figs. 5, 6) furthermore suggests that certain climatic and environmental changes may have caused the extinction of linking species. Alternating glacial and interglacial periods in the vast region of east and southern Africa during the Quaternary caused impressive changes in climate and vegetation (Van Zinderen Bakker, 1983) and this may well have resulted in the extinction of some species of *Raphionacme*. Since modern changes in Africa tend towards increasing aridity, one may surmise an expansion of the distribution range of *Raphionacme*. Much of the present habitat of *Raphionacme* is, however, deteriorating into desert under human influence, and *Raphionacme* may disappear from such areas completely. The incidence of isolated outliers of *R. excisa* and *R. madiensis* may well be examples of such changes. The fact that the tuber and fruit are sources of food to humans further endangers existence of *Raphionacme* in present drought-stricken areas (J.-P. Lebrun, pers. comm.). At present section *Pseudochironia* seems to be the most endangered group.

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POLLEN MORPHOLOGY OF *SARCOCAULON*[1]

R. L. VERHOEVEN AND H. J. T. VENTER[2]

ABSTRACT

Pollen grains of all 14 species of *Sarcocaulon* (DC.) Sweet (Geraniaceae) were examined by light microscopy, scanning electron microscopy, and transmission electron microscopy and have the same basic morphology. The grains are tricolpate, subprolate to spheroidal. The exine structure is reticulate and consists of muri encompassing 5–7 angular lumina. Intraluminal bacula are present in some species. The nexine consists only of nexine I (footlayer).

RÉSUMÉ

Les pollens de 14 espèces de *Sarcocaulon* (DC.) Sweet (Geraniacées) ont été éxaminés à l'aide de microscopie photonique, électronique à balayage, et électronique de transmission; ils ont tous la même morphologie de base. Les pollens sont tricolpés, et subprolés à sphéroïdes. La structure de l'exine est réticulée et consiste en muri qui contiennent de 5 à 7 lumènes angulaires. Des bacules intraluminaux sont présents dans certaines espèces, et la nexine consiste uniquement en une nexine I (footlayer).

Sarcocaulon (DC.) Sweet is one of the five genera of Geraniaceae. The other four are *Erodium* L'Hérit., *Geranium* L., *Monsonia* L., and *Pelargonium* L'Hérit. (Hutchinson, 1969). The Geraniaceae is divided into two tribes, the Geranieae and Pelargonieae. The Geranieae includes *Geranium, Erodium, Monsonia,* and *Sarcocaulon,* the flowers of which are basically actinomorphic, while *Pelargonium,* with zygomorphic flowers, comprises Pelargonieae. Originally *Sarcocaulon* was a section of *Monsonia* (De Candolle, 1824), but Sweet (1926) raised the section to the status of genus, a treatment still followed today.

Sarcocaulon, also known by the common name "Bushman's Candle," comprises 14 species (Moffett, 1979) of perennial, fleshy, short-stemmed shrublets with waxy periderms. The petioles persist as long spines or short blunt stalks. The genus is confined to southern Africa, where it is distributed over the more arid western areas of the Cape Province to eastern Cape, South West Africa/Namibia, and Angola. Of the 14 species, only *S. mossamedense* occurs as far north as Angola. The majority of species occur near the mouth of the Orange River.

The external morphology and nomenclature of the genus have been thoroughly investigated (Rehm, 1935; Merxmüller & Schreiber, 1966; Schreiber & Merxmüller, 1976; Moffett, 1979). The 14 species were divided by Moffett into the following four sections: *Sarcocaulon, Crenati* Moffett, *Denticulati* Moffett, and *Multifidi* Moffett. The division is based primarily on the nature of the leaf margin, a feature considered to be ecologically stable in the genus.

Based on morphological criteria, Moffett (1978) assumed *Sarcocaulon* to be the most primitive genus of the Geraniaceae. Venter (1980), however, is of the opinion that *Monsonia* and *Sarcocaulon* together form the most primitive group in the Geraniaceae and are also nearest in appearance to the ancestral type from which the family evolved.

Palynological characteristics can sometimes provide significant data for the determination of familial relationships (Nowicke & Skvarla, 1977) and infrageneric groupings (Argue, 1981). In a preliminary study of the pollen morphology of the Geraniaceae, Bortenschlager (1967) showed that *Geranium* and *Erodium* cannot be clearly separated by means of pollen morphology and that *Sarcocaulon* and *Monsonia* are pollen morphologically identical. Since the family is under revision [*Monsonia* (Venter, 1979) and *Sarcocaulon* (Moffett, 1979) completed], this study was undertaken as part of a complete palynological investigation of the Geraniaceae. We hope that pollen morphology of *Sarcocaulon* may be useful in a systematic study and in a future clarification of the affinities of the genera in the family.

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TABLE 1. Voucher data for the species of *Sarcocaulon* studied.

Taxon	Collector (all at BFLU)	Grid Reference
Section *Sarcocaulon*		
1 *S. camdeboense* Moffett	*Verhoeven 86*	3225 CA Somerset-East
2 *S. l'heritieri* Sweet	*Verhoeven 88*	2917 BC Springbok
	Verhoeven 69	2917 BA Springbok
	Verhoeven 139	2917 DB Springbok
3 *S. patersonii* (DC.) G. Don	*Venter 8600*	2615 CA Lüderitz
	Verhoeven 89	2916 BB Port Nolloth
	Verhoeven 97	2716 DD Witputz
	Verhoeven 99	2615 CA Lüderitz
4 *S. salmoniflorum* Moffett	*Verhoeven 62*	2818 AC Warmbad
	Verhoeven 98	2616 CB Aus
5 *S. vanderietiae* L. Bol.	*Verhoeven 85*	3327 AA Peddie
Section *Crenati*		
6 *S. ciliatum* Moffett	*Verhoeven 87*	2917 BC Springbok
	Verhoeven 70	2917 BA Springbok
7 *S. crassicaule* Rehm	*Verhoeven 75*	2817 CD Vioolsdrif
	Verhoeven 136	2820 DB Kakamas
8 *S. flavescens* Rehm	*Verhoeven 92*	3017 BC Hondeklipbaai
	Verhoeven 96	2816 DA Oranjemund
Section *Denticulati*		
9 *S. inerme* Rehm	*Verhoeven 95*	2716 DD Witputz
	Verhoeven 149	2716 DD Witputz
10 *S. marlothii* Engl.	*Venter 8597*	2214 DB Swakopmund
11 *S. mossamedense* (Welw. ex Oliv.) Hiern	*Venter 8596*	2113 DD Cape Cross
Section *Multifidi*		
12 *S. herrei* L. Bol.	*Venter 8251*	2917 BB Springbok
	Verhoeven 63	2817 CD Vioolsdrif
13 *S. multifidum* E. Mey. ex Knuth	*Verhoeven 93*	3017 BC Hondeklipbaai
	Verhoeven 144	2816 BC Oranjemund
14 *S. peniculinum* Moffett	*Verhoeven 94*	2816 DA Oranjemund

MATERIALS AND METHODS

Pollen was taken from herbarium sheets (at BLFU), material collected in the field, or from previously collected plants which were cultivated in the Botanical Garden of the University of the Orange Free State. Moffett's (1979) identification of 14 species in *Sarcocaulon* grouped in four sections is followed in this study (Table 1).

For both light microscopy (LM) and scanning electron microscopy (SEM) study, pollen was acetolyzed according to the method of Erdtman (1960). Acetolyzed samples for SEM were rinsed in acetic acid, washed twice in water, air-dried on stubs, coated with gold, and examined with an ISI 100 SEM at 20 kV.

For light microscopy the acetolyzed material was prepared according to the method of Reitsma (1969). Samples were examined with a Zeiss photomicroscope. Measurements of pollen grain size are based on a minimum of 15 grains per specimen. Results of polar diameter were subjected to analysis of variance, and significant differences were identified with the aid of Tukey's test (Steel & Torrie, 1980). A complete set of slides is filed in the Department of Botany, University of the Orange Free State, Bloemfontein.

For transmission electron microscopy (TEM) anthers were fixed in 3% phosphate buffered glutaraldehyde (0.1 mol dm^{-3} phosphate buffer, pH 7.0), postfixed in 1% phosphate buffered osmium tetroxide, dehydrated in ethyl alcohol, and embedded in Spurr's low viscosity resin. Sections were made with a diamond knife using an LKB Ultrotome III microtome, stained with uranyl acetate for ten minutes, followed by three minutes in lead citrate (Reynolds, 1963).

TABLE 2. Size range of pollen grains (mean followed by range in parentheses), colpi, and lumina (μm) in *Sarcocaulon*.

	Polar Diameter	Equatorial Diameter	Colpi	Lumina
Section *Sarcocaulon*				
S. camdeboense	94 (87–102) ± 3.87	88 (83–95) ± 2.79	34.4 × 9.5	8.0
S. l'heritieri	83 (72–96) ± 6.03	78 (68–90) ± 4.90	31.3 × 8.4	6.6
S. patersonii	81 (72–90) ± 5.48	73 (63–81) ± 4.35	33.4 × 8.3	8.1
S. salmoniflorum	65 (57–75) ± 5.23	60 (50–69) ± 5.41	27.9 × 9.3	5.1
S. vanderietiae	89 (81–96) ± 3.28	82 (75–90) ± 5.35	35.5 × 8.4	7.0
Section *Crenati*				
S. ciliatum	75 (65–87) ± 5.99	71 (63–81) ± 3.16	29.5 × 10.7	5.6
S. crassicaule	81 (72–90) ± 5.04	74 (66–83) ± 3.7	31.4 × 8.1	6.0
S. flavescens	76 (63–90) ± 8.21	67 (54–80) ± 7.62	30.3 × 12.0	7.2
Section *Denticulati*				
S. inerme	76 (71–84) ± 3.69	71 (63–77) ± 1.83	33.4 × 9.5	5.9
S. marlothii	82 (72–90) ± 5.12	77 (65–83) ± 3.47	30.9 × 7.1	6.4
S. mossamedense	90 (72–117) ± 12.45	78 (65–99) ± 9.09	31.9 × 7.8	6.3
Section *Multifidi*				
S. herrei	78 (71–84) ± 3.3	72 (66–80) ± 2.91	32.9 × 10.1	6.9
S. multifidum	83 (77–93) ± 4.18	77 (74–81) ± 1.47	38.3 × 7.6	6.2
S. peniculinum	77 (66–95) ± 7.32	70 (63–83) ± 3.78	35.4 × 8.5	7.8

RESULTS

Pollen of all the species of *Sarcocaulon* examined has the same basic morphology. The pollen grains are tricolpate, subprolate to spheroidal. In size (Fig. 1) they range from 65 to 94 μm (polar diameter) and 60 to 88 μm (equatorial diameter) (Table 2). The colpi, with slightly wavy margin, average 27.9–38.3 μm in length, and 7–12 μm in width (Table 2).

The exine structure is reticulate (Figs. 2–43). It consists of muri encompassing 5–7 angular lumina. The lumina average 5.1–8.1 μm in diameter. Muri are straight to slightly wavy and 1.2–3 μm wide. Intraluminal bacula (Fig. 43) are present in some species of *Sarcocaulon*. The number of intraluminal bacula varies from 0–30.

The reticulate exine is divided into sexine and nexine, which are of similar electron density. Sexine layering is, as usual, with sexine attached to nexine by means of bacula which unite into a tectum above. The bacula have a slightly expanded base and gently concave midregion. Sexine is 4.8–6.6 μm thick. The nexine consists only of nexine I (footlayer) (Fig. 44) with traversing channels present. Nexine is 0.5–1.2 μm thick. The intine is well developed around the cytoplasm and is 1.2–2.4 μm thick. Starch grains are present in the cytoplasm.

DISCUSSION

The pollen of *Sarcocaulon* has been classified as the *Monsonia* type (Bortenschlager, 1967). From the work of Bortenschlager (1967) it is clear that the family Geraniaceae is heterogeneous in pollen morphology. The pollen grains of *Erodium, Geranium,* and *Pelargonium* are colporate

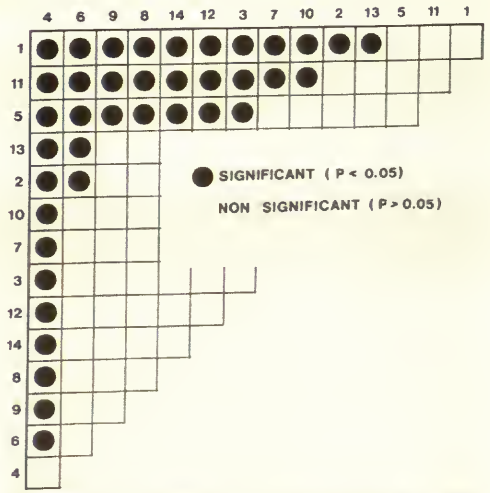
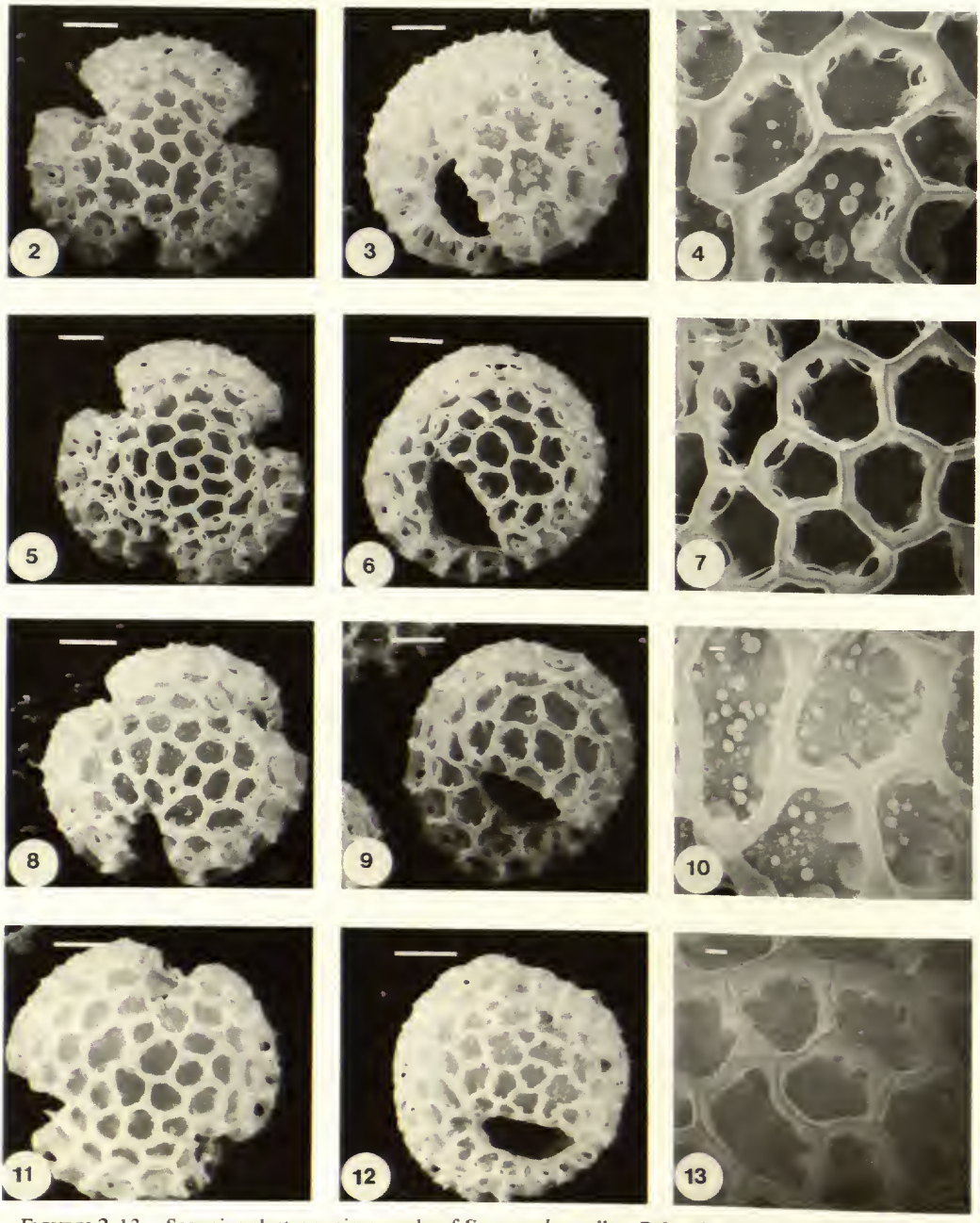


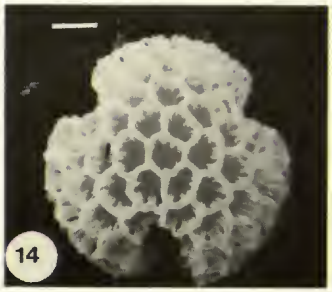
FIGURE 1. Comparison of species differing significantly in pollen dimensions. Numbers correspond to species in Table 1.

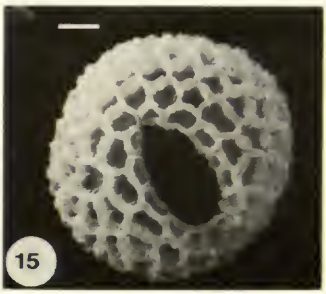


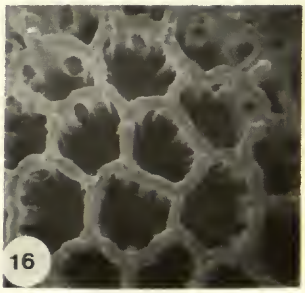
FIGURES 2–13. Scanning electron micrographs of *Sarcocaulon* pollen. Polar view, equatorial view, and detail of reticulate exine.—2–4. *S. camdeboense.*—5–7. *S. l'heritieri.*—8–10. *S. patersonii.*—11–13. *S. salmoniflorum.* Scale in polar and equatorial view equals 10 μm; 1 μm in detail figures.

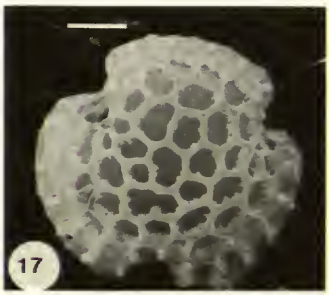
while those of *Monsonia* and *Sarcocaulon* are colpate. The exine is reticulate in all five genera but reticulate to striate in *Erodium* and *Geranium.* Supratectal processes are present in some species of *Geranium* and *Monsonia.* In *Pelargonium* main and second order muri can be distinguished. Pollen size also differs among the genera.

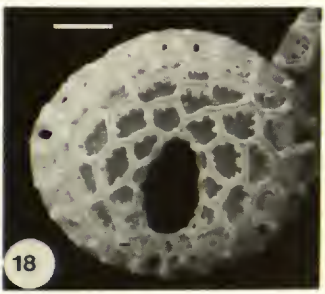
This study of the pollen of *Sarcocaulon* failed to produce diagnostic characters within the ge-

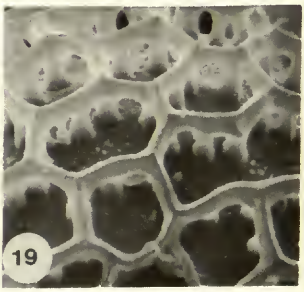


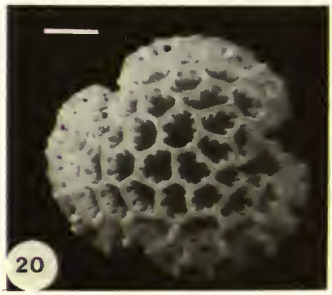


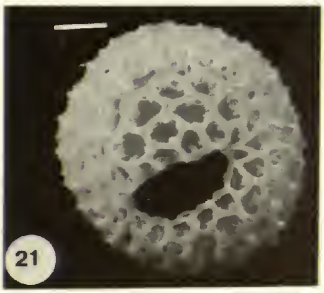


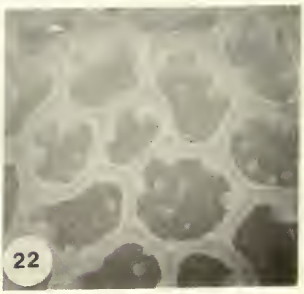


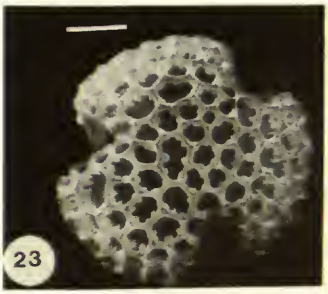


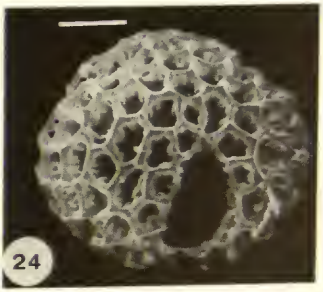


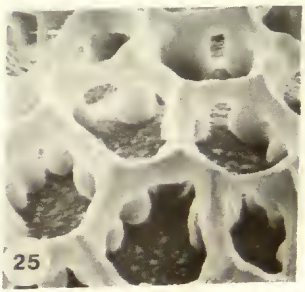








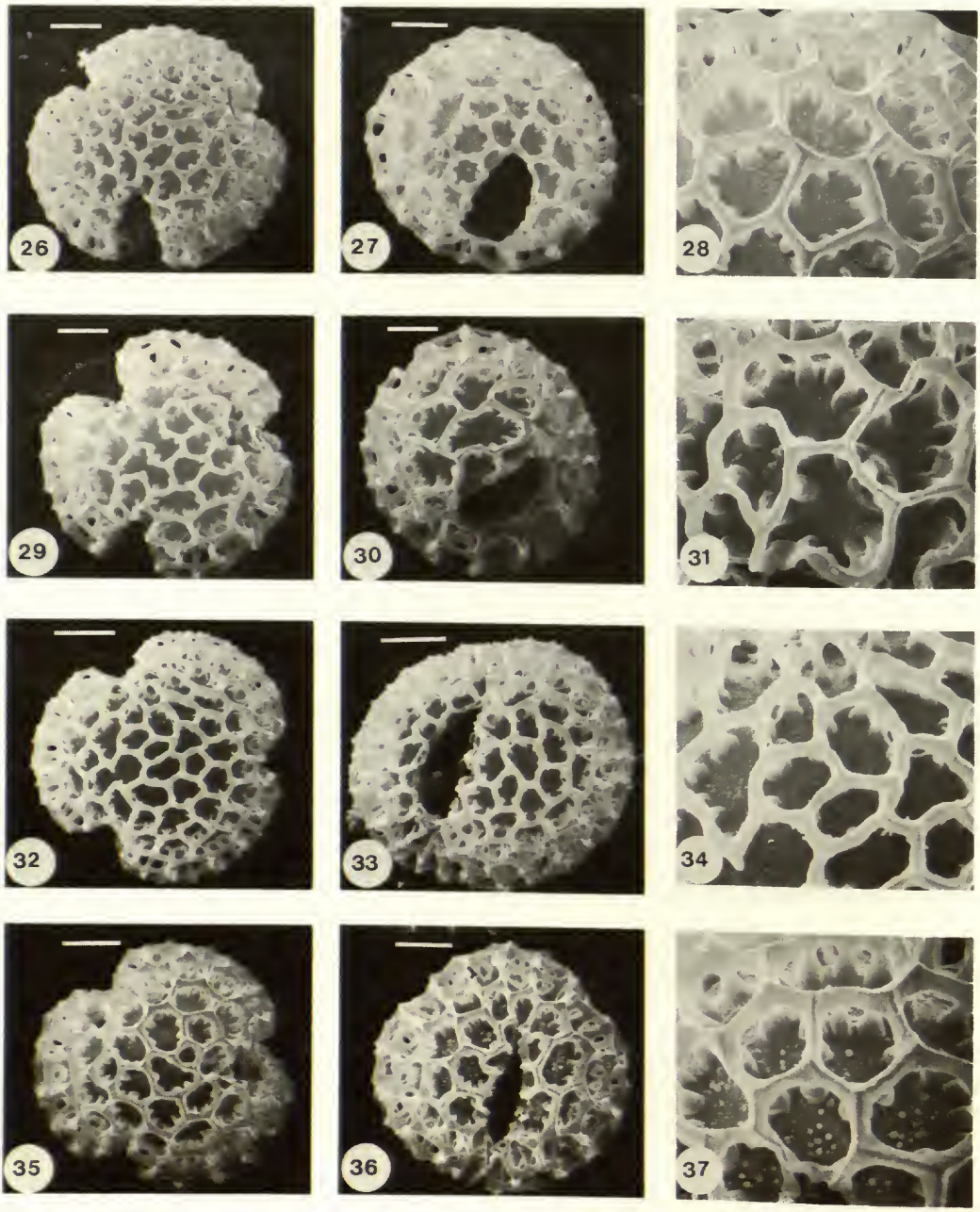




FIGURES 14–25. Scanning electron micrographs of *Sarcocaulon* pollen. Polar view, equatorial view, and detail of reticulate exine.—14–16. *S. vanderietiae.*—17–19. *S. ciliatum.*—20–22. *S. crassicaule.*—23–25. *S. flavescens.* Scale in polar and equatorial view equals 10 μm; 1 μm in detail figures.

nus. Features that might be useful to distinguish between some species are size of grains and presence of intraluminal bacula. Pollen grains are smallest in *S. salmoniflorum* and largest in *S. camdeboense*. Although there is quite an overlap in size between species, some species differ significantly (Fig. 1).

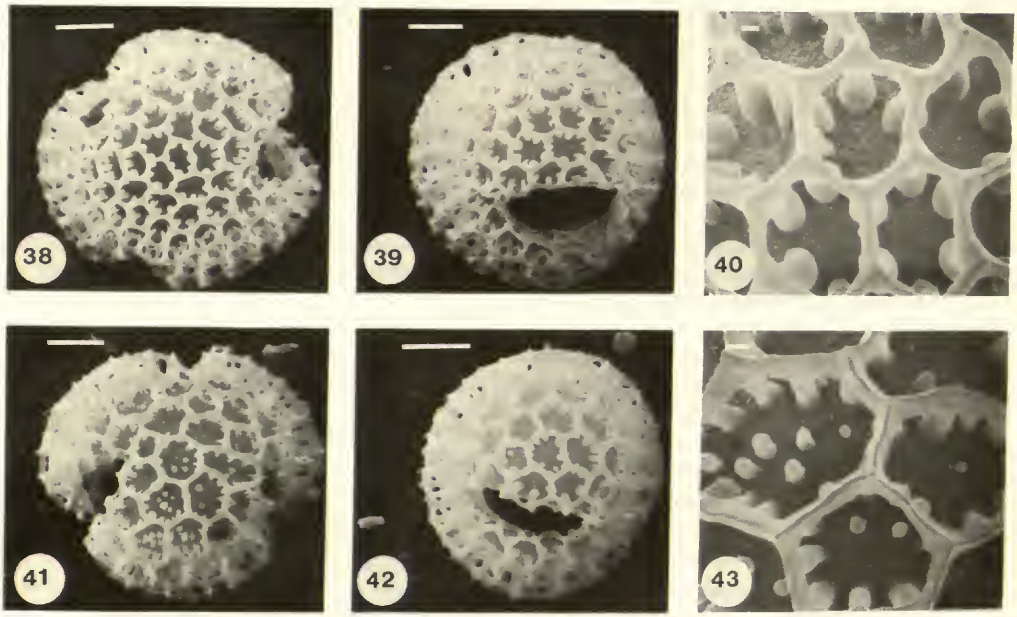
Intraluminal bacula are present in *Sarcocaulon camdeboense, S. ciliatum, S. crassicaule, S. l'heritieri, S. multifidum, S. patersonii,* and *S.*



FIGURES 26–37. Scanning electron micrographs of *Sarcocaulon* pollen. Polar view, equatorial view, and detail of reticulate exine.—26–28. *S. inerme.*—29–31. *S. marlothii.*—32–34. *S. mossamedense.*—35–37. *S. herrei.* Scale in polar and equatorial view equals 10 μm; 1 μm in detail figures.

peniculinum. The intraluminal bacula are most obvious in *S. patersonii* and *S. peniculinum.* These bacula are, however, not a constant characteristic, because they may be present in some grains and completely absent in others. The presence of intraluminal bacula was also observed by Bortenschlager (1967) in *S. l'heritieri, S. patersonii* (as *S. rigidum*), and *S. crassicaule* (as *S. spinosum* var. *spinosum*).

From the work of Bortenschlager (1967) and



FIGURES 38–43. Scanning electron micrographs of *Sarcocaulon* pollen. Polar view, equatorial view, and detail of reticulate exine.—38–40. *S. multifidum.*—41–43. *S. peniculinum.* Scale in polar and equatorial view equals 10 μm; 1 μm in detail figures.

this study, it is clear that due to the presence of a reticulate exine that is similar to that of *Sarcocaulon* and intraluminal bacula, the pollen grains of *Sarcocaulon* and *Pelargonium echinatum* (Thunb.) Curt. are morphologically identical.

According to Baker & Baker (1979), pollen grains of angiosperms must "germinate" on a

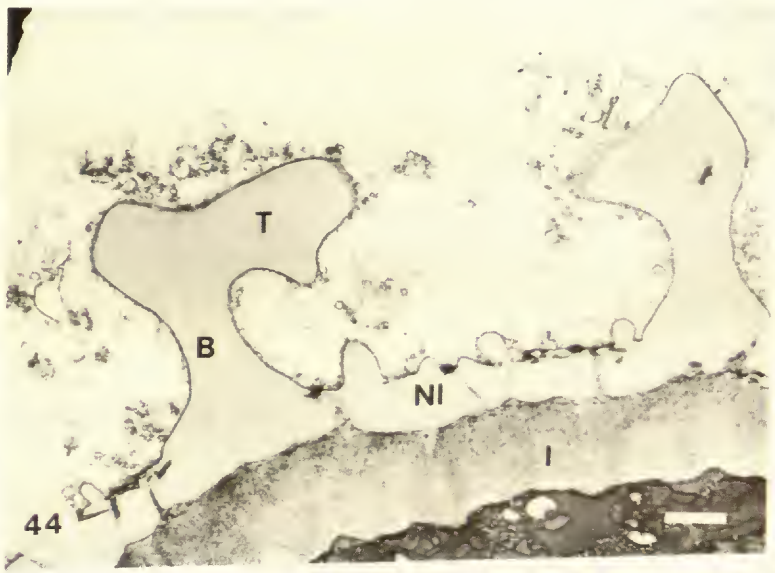


FIGURE 44. Transmission electron micrograph of *S. multifidum* pollen wall. Mesocolpal view. B = bacula; I = intine; NI = nexine 1; T = tectum. Scale bar = 1 μm.

stigma. This growth requires energy, which must be provided initially by reserves in the pollen grain. Such reserves may be in the form of fixed oils, sugars, or starch. In practice, it is possible to distinguish two classes of pollen grains: "starchy" and "starchless." *Sarcocaulon* is characterized by starchy pollen grains, which is in accordance with Baker & Baker's (1979) finding that the Geraniaceae has starchy pollen. In general, members of a particular family are in agreement regarding the possession of starchy or starchless pollen (Baker & Baker, 1979).

This study revealed that pollen morphology cannot be utilized in dividing *Sarcocaulon* into sections or for identifying species, owing to the similarity in morphology. The only characteristics that seem to be of importance are size of grains and presence of intraluminal bacula.

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PROGRESS REPORT ON THE ETHIOPIAN FLORA PROJECT

A short presentation of the Ethiopian Flora Project was given at the tenth plenary meeting of AETFAT (Hedberg, 1983). Progress since the initiation of the project has so far been very good, and by autumn of 1983 most of the manuscripts for the first volume to be printed (Volume III: Rosaceae—Umbelliferae) had been delivered. All manuscripts for that volume are now under editing and we hope that the printing can be started towards the end of 1987. A considerable number of manuscripts for Volume II and further volumes have also been delivered.

Since the start of the project in 1980, 10,000 collections of Ethiopian plants have been made, most of these with four or more duplicates. Collecting trips by purely Ethiopian botanists have added ca. 4,000 of these collections. Major collecting expeditions, involving the project's taxonomic botanists based at Kew and/or collaborators from other European herbaria, together with the Ethiopian staff, have contributed the remaining 6,000 collections.

The first symposium within the project was held in Uppsala in May 1984, with participation from Ethiopian botanists, as well as botanists from various countries collaborating in the project. Following the suggestion by several participants, this symposium was devoted not only to taxonomic problems in the Ethiopian flora but also to general overviews on flora, vegetation, climatology, etc. The proceedings have been published in *Symbolae Botanicae Upsalienses* (XXVI: 2). The second Ethiopian Flora Symposium was held in Ethiopia in November 1986.

Within the project, two Ethiopian students have completed their Ph.D. in plant taxonomy—Mesfin Tadesse ("The Genus *Bidens* (Compositae) in Northeast Tropical Africa") and Sebsebe Demissew ("The Genus *Maytenus* (Celastraceae) in Northeast Tropical Africa and Tropical Arabia"). Two more students have started postgraduate studies in plant taxonomy and one in plant physiology.

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Hedberg, O. 1983. Ethiopian flora project. Bothalia 14: 571–574.

—Olov Hedberg, Department of Systematic Botany, University of Uppsala, Box 541, S-751 21 Uppsala, Sweden; and Mesfin Tadesse, The National Herbarium, Biology Department, Addis Ababa University, P.O. Box 3434, Addis Ababa, Ethiopia.

FLORA OF TROPICAL EAST AFRICA

Since the last report in *Bothalia* 14: 1020–1021 (1983), the following parts of the Flora have been published: Amaranthaceae (C. C. Townsend, 1985), Amaryllidaceae (Inger Bjørnstad, 1982), Anacardiaceae (J. O. Kokwaro, 1986), Ancistrocladaceae (J. Léonard, 1986), Araceae (S. Mayo, 1985), Aristolochiaceae (B. Verdcourt, 1986), Balsaminaceae (C. Grey-Wilson, 1982), Casuarinaceae (M. Wilmot-Dear, 1985), Ceratophyllaceae (M. Wilmot-Dear, 1985), Cruciferae (B. Jonsell, 1982), Cyclocheilaceae (W. Marais, 1984), Erythroxylaceae (N. Robson & B. Verdcourt, 1984), Gramineae, Part 3 (W. D. Clayton & S. A. Renvoize, 1982), Hernandiaceae (B. Verdcourt, 1985), Hydrostachyaceae (B. Verdcourt, 1986), Ixonanthaceae (B. Verdcourt, 1984), Lobeliaceae (Mats Thulin, 1984), Moringaceae (B. Verdcourt, 1986), Myrothamnaceae (Marie Bywater, 1984), Myrsinaceae (P. Halliday, 1984), Nesogenaceae (W. Marais, 1984), Orchidaceae, Part 2 (P. J. Cribb, 1984), Palmae (J. Dransfield, 1986), Rutaceae (J. O. Kokwaro, 1982), Salicaceae (M. Wilmot-Dear, 1985), Triuridaceae (K. Vollesen, 1985), Violaceae (C. Grey-Wilson, 1986), Zingiberaceae (J. M. Lock, 1985), and Zygophyllaceae (M. N. El Hadidi, 1985).

The following parts are in press: Burmanniaceae (E. J. Cowley), Crassulaceae (G. E. Wickens), Dichapetalaceae (F. J. Breteler), Euphorbiaceae and related families (A. Radcliffe-Smith & Susan Carter), Rubiaceae, Part 2 (D. Bridson & B. Verdcourt), and Umbelliferae (C. C. Townsend).

The following parts are with the editor or in an advanced stage of preparation: Aponogetonaceae (K. A. Lye), Balanitaceae (M. J. Sands), Boraginaceae (B. Verdcourt), Celastraceae (N. Hallé, B. Matthew & N. K. Robson), Hydrophyllaceae (B. Verdcourt), Iridaceae (W. Marais), Moraceae (C. C. Berg), Najadaceae (L. Triest), Sapindaceae (F. G. Davies), Simaroubaceae (B. Stannard), and Smilacaceae (E. J. Cowley).

Together, the above parts cover 2,350 species, raising the total to over 6,000 species out of an estimated vascular flora of 9,000–10,000 species. The main residue lies in the Malvales, Gamopetalae, and Liliales sensu lato; but precursory papers are accumulating rapidly for Charles Jeffrey's authoritative account of Compositae, and new initiatives are being made in several of the other large families. Diana Polhill's revised edition of *Index of Collecting Localities* is in an advanced stage of preparation.

Considerable research priority has been given in recent years to this project at Kew and corresponding centers in East Africa. As indicated in the list above, AETFAT members from other institutes have continued to contribute most generously and effectively. The production of the Flora was streamlined by automatic generation of print from coded word-processed text prepared at Kew in 1981, and by in-house typesetting in 1987. Mr. A. T. Balkema has taken a great personal interest in the publication of the Flora, has been assiduous in seeking means to keep down the cost of production, and allowed schemes for subsidized prices to local residents in East Africa.

The above factors depend on a great deal of investment, collaboration, goodwill and hard work. They set a rather more optimistic tone to this report than hitherto. It is proper to emphasize that much remains to be done and that there is a high cost to major floristic projects of this sort, but, nonetheless, the time has come to look forward to the benefits of this undertaking. Most vascular plants from East Africa can be fairly readily identified now. Largely due to the work of Frank White, the vegetational and phytogeographical background is relatively well known. The discreteness, complexity, and interdependence of plants and animals of the wide range of ecosystems in East Africa has become very evident.

Despite a worldwide recession, the 1980s witness considerable advance in techniques and expertise in tropical biology, ecology, conservation, and land use. East Africa is now an extremely attractive area to spearhead multidisciplinary studies.

Some of the exploration and prospective rewards in Tanzania are reviewed by Jon Lovett (this volume). In Kenya, a revised edition of Dale & Greenway, "Kenya Trees and Shrubs" is now well advanced; a second edition of Agnew, "Upland Kenya Wild Flowers" is in preparation; and numerous research projects have been developed in recent years, spearheaded by the visionary aims of the Director of the National Museums and a number of environmental agencies based in Nairobi. Biological programs are also gaining momentum again in Uganda, at least in the western

forests. The governments of several European countries have assisted with research programs, notably the Swedish and Dutch overseas aid organizations; IUCN/WWF have identified Tanzania as a prime target country for their Plants Conservation Program; and the Missouri Botanical Garden has considerably expanded its East African involvement. This is coupled with vigorous expansion of research and development by the local universities, museums and forest departments, with a very real awareness of the urgency for conservation measures and practical development of natural resources.

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